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Modeling Leaf and Inflorescence Development of the African Violet (Saintpaulia ionantha)

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MODELING LEAF AND INFLORESCENCE DEVELOPMENT OF THE AFRICAN VIOLET (*Saintpaulia ionantha* WENDL.)

By

James Emerson Faust

A THESIS

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ABSTRACT

MODELING LEAF AND INFLORESCENCE DEVELOPMENT OF *SAINTPAULIA IONANTHA* WENDL.

By

James Emerson Faust

Models were developed to describe African violet leaf and inflorescence development. Nonlinear functions were used the describe the influence of temperature and daily integrated PPF on the rate of leaf unfolding. Time to anthesis was predicted by integrating two models. The first model predicted the time when a reproductive bud became macroscopically visible in the leaf axil. The second model predicted the time for an inflorescence to develop from visible flower bud to anthesis. The leaf and inflorescence development models were validated in greenhouse experiments with a range of temperatures from 15 to 30C and daily integrated PPF treatments from 2 to 10 mol m^{-2} d^{-1}. The leaf development model predicted leaf number within ± 1 leaf for 85% of observations during an 11 week time period. The inflorescence development model predicted anthesis within ± 5 days for 71% of the observed inflorescences.

DEDICATION

> In the country all was dead still. Little stars shone high up; little stars spread far away in the flood-waters, a firmament is roused and stirred for a brief while by the day, but which returns, and will remain at last eternal, holding everything in its silence and its living gloom. There was no Time, only Space... Where was he? One tiny upright speck of flesh, less than an ear of wheat lost in the field. He could not bear it. On every side the immense dark silence seemed pressing him, so tiny a spark into extinction, and yet, almost nothing, he could not be extinct. Night, in which everything was lost, went reaching out, beyond stars and sun. Stars and sun, a few bright grains, went spinning round for terror, and holding each other in embrace, there in a darkness that outpassed them all, and left them tiny and daunted. So much, and himself, infinitesimal, at the core of nothingness, and yet not nothing.
>
> D.H. Lawrence

To Paul Morel, who had the courage to turn and to walk towards the city's gold phosphorescence.

To Kimberley Brown and to Bob Freeman, who believed in me and also gave me courage to turn and to begin to walk in a new direction.

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Guidance committee:

The paper format was adopted for this thesis in accordance with departmental and university regulations. Section I and II are to be submitted to the Journal of American Society of Horticultural Science.

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LITERATURE REVIEW

Influence of Temperature and Irradiance on Plant Growth and Development

The African violet

Background. *Saintpaulia ionantha* is native to the East African countries of Kenya and Tanzania which are located at 5 degrees south latitude. The average daily temperature in these regions ranges from 24 to 28C, while 0.25 cm of rainfall occurs on approximately 120 days per year. Distribution is limited to a few mountain ranges and a portion of the coastal plain where *Saintpaulia* is found growing on rocks and steep surfaces next to the rain forest epiphytes. Therefore, the natural habitat of the African violet includes relatively warm temperatures, a low PPF, a 12 hour photoperiod, high relative humidity, and frequent watering in a well-drained substrate. (Johansson, 1978)

The African violet was first taken from Africa to Europe in the late 1800's. The genus was named *Saintpaulia* by Hermann Wendlan to commemorate the German baron St. Paul von Illaire. Seed was imported into the United States by 1927, and the first plants were sold in 1936 (Kimmins, 1980). By the 1940s, *Saintpaulia* had become a popular houseplant (Wilson, 1951), and scientific research had been initiated (Poesch, 1943; Elliott, 1947). In 1990, 23 million pots were sold in the United States

at a total wholesale value of more than 27.6 million dollars (Anonymous, 1990). The success of *Saintpaulia* has been due to the relative ease with which it can be grown both in a commercial greenhouse and in a home environment, and also the many unique flower and foliage types which both professional and amateur breeders have developed.

The African violet has a rosette growth habit with the leaves growing in a whorl on a compact stem. The leaves have been bred to display many different shapes which range from ovate to undulate (Wilson, 1951). The apical meristem grows indeterminately while the axillary meristems can differentiate into either vegetative shoots or reproductive inflorescences. The five-petaled flowers can be various shades of violet, pink, white, or a mixture of these colors, termed bi-color.

Commercial production. Commercial production typically begins with the propagation of leaf cuttings (von Hentig, 1976). Propagation can also be accomplished by seed or tissue culture. Seed propagation is not commonly used because most of the varieties do not come true to seed. Much research has been done on micropropagation (Vazquez and Short, 1978; Start and Cumming, 1976; Bilkey and Cocking, 1981; Cooke, 1977); however, micropropagation has not had much commercial significance due to economic limitations.

Stock plants supply the leaf cuttings for propagation. Leaves are removed after they are at least 3 cm long. The petioles are removed, and the leaves are inserted 1 to 2 cm deep into a soilless medium. Roots form endogenously from cells lying between the leaf traces, followed by shoots which develop exogenously from the epidermal cells (Naylor and Johnson, 1937). Anywhere from 1 to 10 plantlets will develop from one leaf cutting (Sanderson and McGuire, 1988). After the plantlets have

emerged from the medium, the mother leaves, i.e. the leaves from the cuttings, are torn off at the medium surface in order to allow more light to reach the developing plantlets.

Growth regulators, specifically cytokinin (PBA) and Gibberellic acid together, applied to developing shoots 1 cm long resulted in a 43% increase in the number of transplantable plantlets which developed from each leaf cutting (Sanderson and McGuire, 1988). Use of either chemical is not practiced commercially.

Plantlets are separated when they have reached sufficient size for transplanting, i.e. the stem diameter is 3 mm or greater, and 4 to 5 leaves have unfolded. Two or three leaves are removed from each plantlet to allow tight spacing between the plug cells. The roots are then removed in order to increase the ease with which the plantlets are planted and also to increase the uniformity of development between plants. The plantlet is inserted into an individual cell (22 cm^3), whereupon the roots regenerate from the stem in about one week. Rooted plantlets are termed plugs. After approximately 8 weeks, the plugs which have approximately 10 unfolded leaves are transplanted into the final growing container, most typically a 10 cm diameter pot (450 cm^3).

Many growers purchase plugs to avoid propagation. The flowers usually begin to appear in the leaf axils near the time when the plants are transplanted from the plug to the 10 cm pot. The plants will flower and be ready for sale in 7 to 10 weeks. A saleable plant will typically have 20 leaves and 2 to 3 inflorescences each with one or more open flowers. The wholesale value is approximately $1.25 (Personal communication, Post Gardens Greenhouse). Total production time from leaf cutting to sale requires 8 to 10 months.

Influence of the greenhouse environment on growth and development. Research on the African violet has focused on identifying the influence of the greenhouse environment on plant morphology and growth. Environmental factors examined in this review include temperature, irradiance, carbon dioxide, and relative humidity. Morphological data usually includes, leaf size, leaf number, flower number, inflorescence number, and flower number per inflorescence. Growth is measured as total plant dry weight and/or fresh weight accumulation.

Temperature. Went concluded in his classical study of plant growth (1957), that optimal growth, indicated by plant height or time to flower, occurred for most plants with a day temperature (DT) 5C higher than the night temperature (NT). However, an exception was noted for *Saintpaulia ionantha* which flowered earliest at a DT of 14C and NT of 20 to 23C. This observation has since been published in many botany and horticulture texts (Leopold and Kriedemann, 1975; Larson, 1980; Mastalerz, 1977). While Dvorska (1979) claimed to confirm Went's observation, no data were presented to support the conclusion.

Hildrum and Kristoffersen (1969) examined the effect of DT, NT, and photosynthetic photon flux density (PPF) on African violet by measuring plant fresh weight and the number of flowers produced per plant. They found that growth and flowering were a function of average daily temperature (ADT). Fresh weight and flower number increased as temperature was increased from 15 to 24C, and then decreased as temperature was increased further to 27C. Decreasing either the DT or NT resulted in decreased fresh weight and flower number.

Went (1957) also observed an interaction between temperature and illuminance; i.e. as illuminance increased, the optimal temperature for growth and flowering decreased. Hildrum and Kristofferson (1969) also reported an interaction between temperature and illuminance. They found that more flowers were produced on plants grown at an air temperature of 24 to 27C when the illuminance level was 4 to 8 klx for 16 h (3.1 and 6.2 mol m^{-2} d^{-1}) from cool white fluorescent (CWF) lamps, then on plants grown under 12 klx for 16 h (9.3 mol m^{-2} d^{-1}). The optimal temperature for flowering was 21 to 24C, while flowering was inhibited at 27C. However, plant temperature was not reported. It is possible that sufficient heating from thermal radiation occurred on plants grown at the 9.3 mol m^{-2} d^{-1} treatment that the plant temperature was raised above the optimal temperature, which resulted in decreased flower number.

Vogelezang (1988) used the African violet to study the effect of root-zone heating on inflorescence fresh weight and flower number per plant. She observed that elevating root-zone temperature from 17 to 25C increased inflorescence fresh weight and flower number. However, her data are inconclusive with respect to determining whether the observed increase in growth was due to the increased root temperature or the increased stem or leaf temperature. Plant meristem temperature was more closely correlated to soil temperature than to either leaf or air temperature. *Saintpaulia* is a species which has a relatively large stem diameter and a meristem usually less than 4 cm from the soil surface; therefore, conductive heat transfer between the stem and the soil can significantly affect meristem temperature and consequently plant development rate.

Being of tropical origin, the African violet is sensitive to low temperature and chilling injury. Larcher and Neuner (1989) determined the threshold temperature for

chilling injury in African violet to be between 9 and 10C. Bodnar and Larcher (1987) showed African violet organs varied in their degree of sensitivity to cold temperature (6C for 9 days). The leaves were the most susceptible organ, while the petioles, stem, and shoot apex were less susceptible. Different tissues in the leaves also varied in their susceptibility to chilling. The palisade parenchyma cells were the most susceptible while the spongy parenchyma, upper epidermis, and lower epidermis were less susceptible. Pollen were much less sensitive than the ovules in the flowers. Preconditioning of the African violet at 15C DT and 11C NT for one week resulted in a 30-40% decrease in the amount of irreversible damage to plants placed at 6C for 9 days.

"Ring spot" is the appearance of circular white spots on the foliage of African violets. Poesch (1943) showed cold water being splashed on warm leaves to be the cause of "ring spot". Elliott (1947) confirmed Poesch's report and concluded that water which was 5 to 10C colder than the leaf temperature would cause the collapse of the palisade parenchyma cells in the leaf. The other leaf tissues remain unaffected.

Irradiance. The African violet is a shade plant (Johansson, 1978); therefore, the acceptable irradiance level for *Saintpaulia* is lower than for many other greenhouse crops. Research has focused on the importance of light on the flower development of African violets. Stinson and Laurie (1954) microscopically examined crosssections of leaf axils of plants grown at a range of irradiance levels over a 3 month period of time to determine the minimum irradiance level required for flower initiation and development. They found that floral organs failed to initiate and/or fully develop on plants grown with less than 500 footcandles (100 μmol m^{-2} s^{-1}) during the peak light intensity of a day in October through December.

Hanchey (1955) measured the number of flowers, leaves, and inflorescences on plants grown under CWF lamps which delivered 100, 300, or 600 footcandles (15, 44, and 88 μmol m^{-2} s^{-1}) for 6, 12, or 18 h (0.32 to 5.7 mol m^{-2} d^{-1}). The results indicated that flower number, leaf number, and the number of inflorescences per plant were a function of the daily integrated PPF. The manner in which the irradiance was delivered was not critical. The number of leaves per plant and the number of flowers per inflorescence increased as the daily integrated PPF increased up to 3.6 mol m^{-2} d^{-1}. Increasing the daily integrated PPF above 3.6 mol m^{-2} d^{-1} did not result in any further increase in leaf number or the number of flowers per inflorescence. The number of inflorescences per plant and the number of flowers per plant increased as daily integrated PPF was increased up to 5.7 mol m^{-2} d^{-1}. In an experiment conducted under natural irradiance, daily integrated PPF above an estimated 5.2 mol m^{-2} d^{-1} resulted in decreased plant size, e.g. shorter petioles and smaller leaves.

Hildrum and Kristoffersen (1969) observed that fresh weight increased as the illuminance from CWF lamps increased from 4 to 8 klx for 16 h (3.1 to 6.2 mol m^{-2} d^{-1}), but increasing the illuminance to 12 klx for 16 h (9.3 mol m^{-2} d^{-1}) did not result in any further increase in fresh weight. However, flower and bud number increased from 23 to 39 per plant as the daily integrated PPF increased from 3.1 to 9.3 mol m^{-2} d^{-1}.

Mortensen (1983) found that increasing the PPF from 38 to 100 μmol m^{-2} s^{-1} for 16 h (2.2 to 5.5 mol m^{-2} d^{-1}) resulted in increased dry weight, leaf number, and flower number per plant.

Light quality influences plant growth and morphology. Cathey et al. (1978) examined the effects of seven different fluorescent lamps on African violets. Lamp type

significantly affected fresh weight, but did not affect leaf length or node number. Irradiance at canopy level for the different lamps ranged from 14 to 23 W m^{-2} (400 to 700 nm) for 16 h (3.7 to 5.8 mol m^{-2} d^{-1}). However, daily integrated PPF did not appear to affect fresh weight or leaf length. Fresh weight was significantly affected by the lamp type. The number of days to flower decreased with the addition of incandescent lighting with CWF lamps. However, thermal barriers were not placed above the plants in this experiment; therefore, the increased amount of long-wave radiation due to the incandescent lamps may have increased plant temperatures. Hanchey (1955) found that the number of flowers per inflorescence was higher, total plant width was longer, and fewer vegetative lateral shoots developed on plants grown under CWF lamps compared to sunlight.

Conover and Poole (1981) placed flowering African violets into environments with illuminances of 0.5, 1.0, and 2.0 klx for 12 h (0.3, 0.6, and 1.2 mol m^{-2} d^{-1}) supplied by CWF lamps. All of the plants in the 0.3 and 0.6 mol m^{-2} d^{-1} treatments had stopped flowering after three months, while 38% of the plants in the 1.2 mol m^{-2} d^{-1} treatment were still flowering. After 9 months, 3, 62, and 100% of the plants were flowering in the 0.3, 0.6, and 1.2 mol m^{-2} d^{-1} treatments, respectively. Conover and Poole concluded that the African violet has the ability to acclimate and flower under illuminances as low as 1.0 klx for 12 h (0.6 mol m^{-2} d^{-1}) and to continue vegetative growth even at illuminances as low as 0.5 klx for 12 h (0.3 mol m^{-2} d^{-1}). Different rates of nitrogen, 0, 6, 12, and 24 mg per pot, were applied to the plants in the post-harvest environment; however, nitrogen rate did not influence leaf or flower development.

High PPF can cause destruction of chlorophyll in the leaves of African violets. Carpenter (1969) measured chlorophyll content of plants grown under shade cloth (maximum illuminance was 1500 footcandles, or 300 μmol m^{-2} s^{-1}) and direct sunlight (maximum illuminance was 6685 footcandles, or 1337 μmol m^{-2} s^{-1}) and measured 30 and 7 mg/100 g fresh weight for the respective treatments. He also observed that the breakdown of chlorophyll and foliar burn increased as leaf temperature increased. Hildrum and Kristoffersen's (1969) visual observations confirmed that PPF is the main factor affecting foliar burn and that higher leaf temperature can accentuate the amount of foliar burn which occurs. Raabe (1957) claimed that temperature difference between the leaf and applied water, time of exposure to cold water, the wavelength of light, as well as the PPF could cause chlorophyll degradation in the African violet. Also Raabe reported that more highly pigmented varieties were more resistent to high light-induced foliar burn; however, data were not presented. The PPF at which chlorophyll breakdown begins to occur in the African violet has not yet been identified.

Carbon dioxide. Greenhouses can become depleted of carbon dioxide especially during sunny winter conditions when photosynthesis rate is high and greenhouse air is not being exchanged with outside air (Mastalerz, 1977). Enriched carbon dioxide environments have been shown to increase plant dry weight gain (Owen et al. 1926; Wittwer and Robb, 1964). Therefore, supplementary carbon dioxide can be added to the greenhouse air to improve plant growth.

Mortensen (1983) studied the effect of carbon dioxide enriched air on African violet and found that increasing carbon dioxide concentration from 330 to 600-900 μl l^{-1} while the daily integrated PPF was maintained at 3 mol m^{-2} d^{-1} resulted in earlier

flowering, more flowers, more flower buds, and dry matter production was increased 19.7 to 38.6%. Carbon dioxide concentrations above 900 μl l^{-1} gave no additional effect on growth. Mortensen (1986) also found that continuous enrichment with carbon dioxide was superior to intermittently supplying carbon dioxide.

Although African violets respond strongly to an enriched carbon dioxide atmosphere, the measured benefits in dry weight gain and earlier flowering do not reflect the loss of perceived plant quality. Specifically, carbon dioxide concentrations above 600 μl l^{-1} result in thicker and more brittle leaves. Brittleness increases the amount of damage which occurs to the plants during shipping and handling. Therefore, a carbon dioxide concentration of 600 μl l^{-1} is recommended for greenhouse production (Fischer, 1989).

Relative humidity. Mortensen (1986) observed that increasing the relative humidity from 55-60% to 90-95% resulted in a 17 to 36% increase in dry weight. The increase in dry weight was due to an increase in leaf number and leaf size. Time to flower was decreased by 2 to 3 weeks, the number of flowers and flower buds per plant increased by 33%, and dry weight increased 20% as relative humidity was increased. Similar results have been identified on many other species: chrysanthemum, Boston fern, rose, Hiemalis begonia (Mortensen, 1986), tomato (Mitchell and Hoff, 1977), lettuce (Tibbitts and Bottenberg, 1976), kale and sugar beet (Ford and Thorne, 1973).

Leaf Development.

Phenology. Development refers to qualitative changes in plant structure, such as the differentiation of vegetative and reproductive tissue. Plant development can be

divided into different developmental stages which are identifiable by morphological characteristics, such as the third-leaf stage or visible flower bud. Phenology is the study of these developmental stages as influenced by the environment and genotype.

Phasic development scales of specific crops have been created to separate the different phases of crop development. Scales, such as for the sunflower (Table 1) and for wheat (Figures 1 & 2), were developed to identify the status of phenological development and to provide a numerical definition to the growth occurring between stages of development. Phenological scales have been used extensively to study the effect of the environment on plant development (Baker et al., 1986; Boone et al., 1990; Cudney, 1989).

Phenological scales are usually more useful for studying the development of container-grown ornamental plants than quantitative analysis of growth, i.e. fresh and dry weight accumulation. The measure of a container-grown ornamental plant is more closely determined by phenological description, while quantitative analysis of growth is more useful in modeling the growth of crops in which a portion of the plant is harvested, e.g. agronomic crops, vegetables, and cut flowers.

Phenological models are usually based upon studies of developmental stages as isolated processes, i.e. the assumption is made that the preceding phase has no effect on the current stage of development. However, Karlsson et al. (1989) showed that high and/or low temperatures occurring during early stages of chrysanthemum development delayed development in later stages.

Table 1. Phenological scale describing the development of the sunflower (Schneiter and Miller, 1981).

Sunflower (*Helianthus annuas* L.)	
Growth stage	Description
Vegetative	Emergence: first true leaf blade <4 cm long
VE	First true leaf 4 cm long
V1	Second leaf
V2	Third leaf
V3	n number of leaves
Reproductive	
R1	Inflorescence surrounded by immature bracts becomes visible
R2	Internode below base of inflorescence elongates 0.5 to 2.0 cm above leaves
R3	Growth of internode below reproductive bud lifts inflorescence >2 cm above leaves
R4	Inflorescence begins to open
R5	Beginning of anthesis
R6	End of anthesis
R7	Back of inflorescence starts to turn light green
R8	Back of head is yellow but bracts remain green
R9	Physiological maturity; bracts become yellow and brown

The optimal temperature for development can be unique for each stage of development. Karlsson et al. (1989) identified the optimal temperature for chrysanthemum to be 23.1C from the time of disbud to flower bud color and 19.1C from flower bud color to anthesis.

Figure 1. Development of a wheat leaf (leaf number 7) in 0.1 units, from 7.0 to 7.9. The unit designation is determined by the approximate length of the seventh leaf (on left) relative to the sixth leaf (at right) (Haun, 1973).

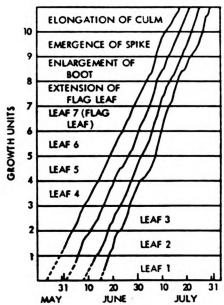

Figure 2. Cumulative development of four plantings of Spring wheat (Haun, 1973).

Angus et al.(1981) showed that the base temperature in wheat was 2.6C from sowing to emergence and 8.9C from anthesis to maturity. The leaf appearance rate (LAR) of maize increased from 0.29 to 0.42 leaves d^{-1} as the plant age increased from 35 to 43 days after emergence to 43 to 50 days after emergence (Tollenaar, 1984). Karlsson et al. (1988) did not observe any change in LAR during the development of Easter lily; however, the LAR of *Hibiscus* (Karlsson et al., 1991) and wheat (Boone et al., 1990) decreased as the species changed from vegetative to reproductive development.

Temperature. Temperature is the primary variable used to predict rates of development (Kiniry et al., 1991), while photoperiod (Major et al., 1978), light intensity (Friend et al., 1962), water stress (Hodges and French, 1985), and nutrition (Snyder and Bunce, 1983) have also been included in plant development models.

Vegetative development is often quantified by measuring LAR. LAR refers to the reciprocal of the number of days required for one leaf to visually appear, or unfold, at the apical shoot. LAR varies considerably between species (Table 2) and also between cultivars of the same species (Tollenaar et al., 1984; Snyder and Bunce, 1983).

LAR has a base temperature or threshold at which increased temperature results in a linear increase of LAR until an optimum is reached at which point a further increase in temperature results in a rapid decrease in LAR. The highest rate of development for any average daily temperature occurs at a constant day and night temperature (Erwin and Heins, 1990; Coligado and Brown, 1975). Fluctuating temperatures result in a slower rate of development whenever temperatures occur outside of the linear temperature range (Erwin and Heins, 1990). Development results from the accumulation of responses to small time intervals. As a result, more frequent measurements

Table 2. Comparison of T_{Min}, T_{Opt}, and the interval between the appearance of leaves at T_{Opt}.

Species	T_{Min}	T_{Opt}	Interval between leaves appearing at T_{Opt} (days)	
Banana	8	27	10.3	(Allen et al., 1988)
Hiemalis Begonia	11	22	6.2	(Faust and Heins, 1990)
Hibiscus	8	31	4.3	(Karlsson et al., 1991)
Wheat	0	25	4.0	(Baker et al., 1986)
Maize	8	32	1.6	(Watts, 1972)
Chrysanthemum	0	30	1.8	(Karlsson et al., 1989)
Sunflower	-	-	1.1	(Rawson and Hindmarsh, 1982)
Sugar beet	1	20+	1.7	(Milford et al., 1985)
Easter lily	1	30	0.4	(Karlsson et al., 1988)

of the plant environment should be more useful in predicting development over a longer period of time (Karlsson et al. 1991). However, Gilmore and Rogers (1958) and Cross and Zuber (1972) did not observe any improvements in predicting development using 3 hour, and hourly temperatures in degree-day models. The temperature range provided during these experiments may not have frequently risen above the linear temperature range.

Irradiance and Photoperiod. The results from investigations of the effect of PPF and photoperiod on LAR have varied between experiments. The LAR of sunflower decreased 11% as solar radiation was decreased by 50% (Rawson and Hindmarsh, 1983). The LAR of maize increased up to 20% at 18C as PPF was increased from 27 to 36 mol m^{-2} d^{-1}; however, no change in LAR was observed when the same experiment was conducted at 28C (Warrington and Kanemasu, 1983). LAR of wheat

(Friend et al., 1962) did not change as photoperiod increased from 8 to 16 hour and a similar daily integrated PPF was provided to both treatments.

Experiments conducted to study the effect of photoperiod often neglect to deliver the same daily integrated PPF to the photoperiod treatments which makes it impossible to separate the effects of light quantity and photoperiod. Aspinall and Paleg (1964) found no significant change in LAR on barley as photoperiod increased from 10 h and a daily integrated PPF of 6.2 mol m^{-2} d^{-1} to 16 h and a daily integrated PPF of 20 mol m^{-2} d^{-1}; however, Cao and Moss (1989) observed a 20 and 33% increase in LAR of wheat and barley respectively as photoperiod increased from 8 h and a daily integrated PPF of 12 mol m^{-2} d^{-1} to 24 h with a daily integrated PPF of 35 mol m^{-2} d^{-1}.

The LAR of soybeans grown under an 8 h photoperiod increased 9% as PPF was increased from 500 to 1000 μmol m^{-2} s^{-1} (14.4 to 28.8 mol m^{-2} d^{-1}), while the LAR increased 14 to 33% when PPF was held constant at 500 μmol m^{-2} s^{-1} and the photoperiod was increased from 10 to 16 h (18 and 28.8 mol m^{-2} d^{-1}) (Snyder and Bunce, 1983). An increase in photoperiod from 10 to 14 h resulted in a 25% increase in LAR of banana (Allen et al., 1988); however, PPF was not reported.

Flower development.

Flower induction, initiation, and development can be positively and negatively influenced by several environmental factors, including temperature, PPF, photoperiod, nutrition, and water stress. This review focuses on the effects of temperature and irradiance on the flowering process.

Flower development can be quantified by measuring the number of flowers which develop per inflorescence, stem, or plant, or the time required for a plant to develop to anthesis. The reciprocal of the time to anthesis provides a measure of rate of development.

Phenological scales can be used to describe the changes which occur to a vegetative meristem as reproductive organs differentiate (Figure 3). Scales can also be used to describe the visible development of the inflorescence (Figure 4).

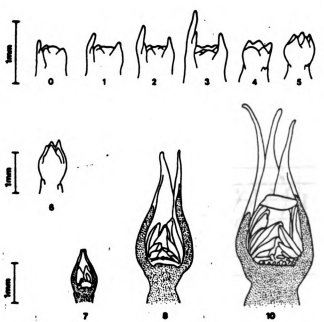

Figure 3. Developmental stages of a reproductive apex of the rose. Cut surfaces are shown stippled (Horridge and Cockshull, 1974).

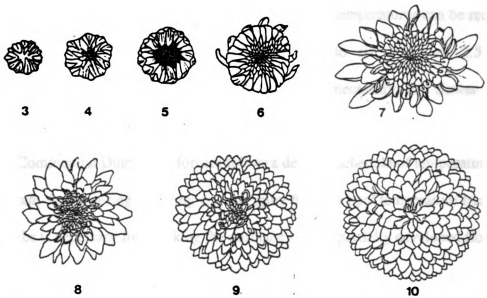

Figure 4. Developmental stages of chrysanthemum flowers. Stages 8 to 10 are drawn at half the scale of stages 3 to 7 (Cockshull and Hughes, 1972).

"Bud meters" provide a method of predicting anthesis as a function of flower bud size and temperature (Figure 5).

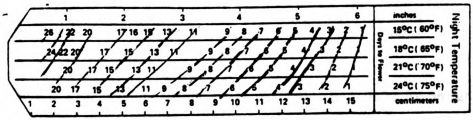

Figure 5. Bud development meter as computed from regression equation: Days to flower = 33.258 - 2.039 * Bud length - 0.736 * Temp. + 0.044 * Temp. * Bud length (Healy and Wilkins, 1984).

Temperature. Both relatively warm and/or cool temperatures can be required for flowering. *Lilium longiflorum* bulbs require four to six weeks of 2.5 to 5.0C temperatures to provide the vernalization treatment necessary for flower induction (Lange and Heins, unpublished data).

Commercial Dutch bulb forcers follow a detailed schedule of temperature regimes to program the flowering of spring crops (Figure 6). The cool temperature treatment for tulip bulbs is necessary for breaking the dormancy of the partially developed flower buds.

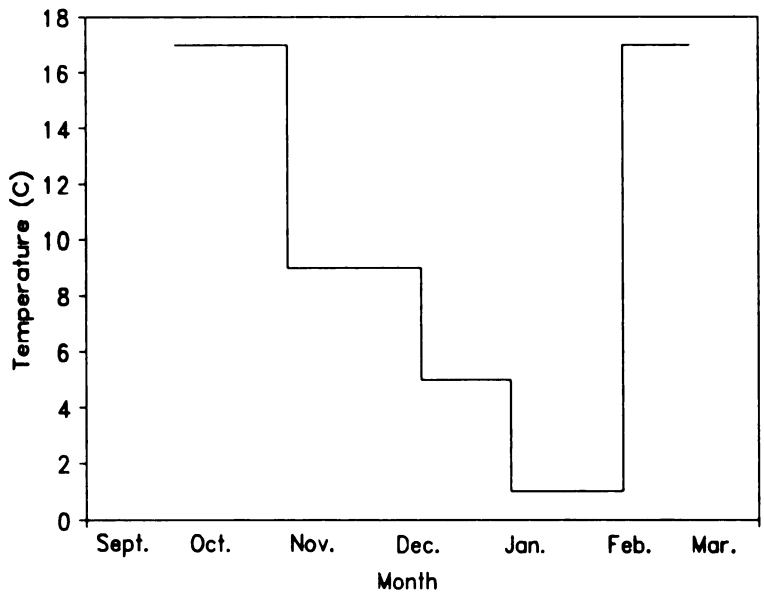

Figure 6. Temperature regime for programming tulip bulbs for an early March sales date (Dehertog, 1989).

The response of flower development to temperature is similar to the response of leaf development. Below a threshold temperature flower development fails to proceed. Above the threshold, development increases linearly with respect to temperature until an

optimal temperature is reached. Flower development decreases rapidly at supraoptimal temperatures.

The optimal temperature for flowering can be considerably different than for leaf development of the same species. The optimal temperature for flower development of chrysanthemum was 21C, while the optimal temperature for leaf development was 30C (Figure 7).

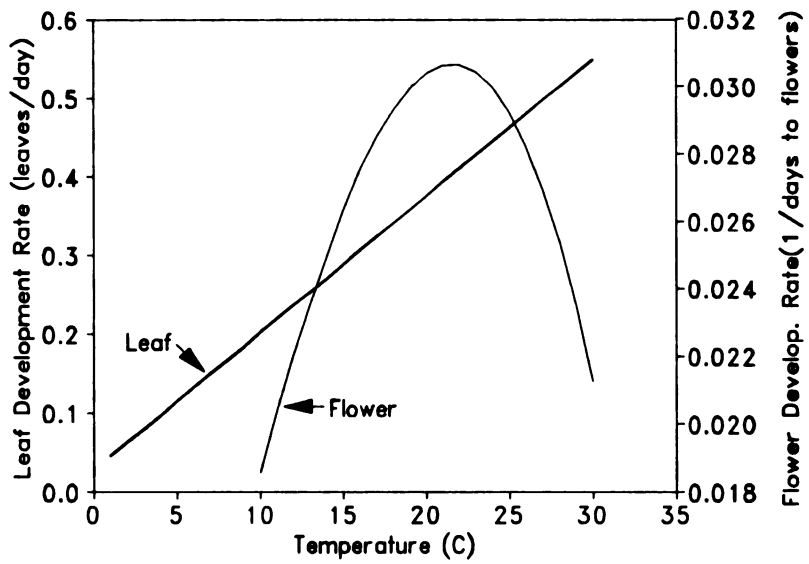

Figure 7. Comparison of temperature responses for leaf and flower development of chrysanthemum (Karlsson et al., 1989; Karlsson et al., 1990).

The optimal temperature for flower development may not be the optimal temperature for the growth of the floral parts. For example, geranium inflorescences developed most rapidly at 28C, while the largest flower petals were observed at 18C (Armitage et al., 1981).

Time to anthesis is usually described as a function of ADT; however, high NT can affect flowering independent of DT. Poinsettia flower initiation was delayed by 21C NT in one study (Kofranek and Hackett, 1966) and 23C NT in another study (Berghage et al., 1987); however, 29C DT did not delay flower initiation or development (Berghage, et al., 1987).

The sensitivity of flower development to temperature can change during the course of development. For example, the number of aborted gladiolus flower buds increased when exposed to high temperature (50C) immediately after the corm was planted or at the appearance of the fifth leaf onward. The flower bud abortion which occurred during the later stage was increased under a low relative humidity environment (40-50%) indicating that the apparent effect of temperature may be caused by water deficit (Shillo and Halevy, 1976).

Harris and Scott (1969) found that development of carnation flowers was a function of bud temperature when bud and leaf temperature were varied independently. Flower buds which were 9C warmer than leaf temperature flowered 26 days sooner than plants grown with the leaves 9C warmer than the flower buds.

Irradiance. The rate of flower development with respect to irradiance follows a classical asymptotic response. The threshold daily integrated PPF, below which flower development is significantly delayed or completely inhibited, for a number of different species are shown in Table 3.

Moe (1972) observed on roses that as illuminance was increased from 1.5 to 12 klx for 24 h (1.8 to 14.4 mol m^{-2} d^{-1}), the number of days to flower decreased from 67 to 48, the number of flowers per shoot increased from 1.9 to 3.4, and shoot length

Table 3. The daily integrated PPF at which flower initiation and development cease to occur for four species.

Species	Integrated PPF (mol m^{-2} d^{-1})	
Fuchsia	3.8	(Sachs and Bretz, 1962)
Geranium	1.9	(Armitage et al., 1981)
Azalea	2.3	(Bodson, 1983)
Chrysanthemum	1.1	(Cockshull and Hughes, 1972)

decreased from 27 to 20 cm. Moe and Kristoffersen (1968) also reported that increasingilluminance from 2 to 10 klx for 16 h (1.5 to 7.8 mol m^{-2} d^{-1}) did not change the number of petals per flower, while the number of blind shoots decreased by 58%. Horridge and Cockshull (1974) suggested that the effect of light on rose development was that light released the correlative inhibition of the axillary buds. The number of flowering shoots was directly related to the number of developing lateral shoots; therefore, high irradiance conditions increased the number of axillary buds which developed and thus the number of flowers which developed.

Flower abortion occurs when unfavorable environmental conditions, such as low irradiance or low temperature, occur during flower development. Tomatoes are most sensitive to low irradiance conditions at the stage of inflorescence development when the peduncle is lengthening and the floral organs are growing, i.e. the macroscopic appearance of the inflorescence (Kinet, 1977). In chrysanthemum, low daily integrated PPF during the first two weeks of flower initiation caused the greatest delay in flowering, but once the receptacle and bracts began to development, the inflorescence continued to

develop, albeit slower, even when plants were grown at daily integrated PPF at which flower initiation failed to occur (Cockshull and Hughes, 1972).

In geranium, the number of days from germination to visible flower bud decreased 33% as the PPF increased from 50 to 375 μmol m^{-2} s^{-1} during an 18 h photoperiod (3.2 to 24.1 mol m^{-2} d^{-1}); however, the same PPF range did not affect the time from visible flower bud to anthesis. The high PPF possibly induced the flowering process by expanding the photosynthate pool; after which, temperature controlled the rate of development (Armitage et al., 1981).

In gladiolus 'San Souci', reducing the natural irradiance by 25% resulted in a 27% decrease in the number of flowering plants and 53% decrease in the number of florets per spike. The stage of development from the fifth leaf to spike emergence was the most sensitive to irradiance reduction, i.e. resulted in the greatest reduction in percentage of flowering plants and number of florets per spike (Shillo and Halevy, 1976).

Hughes and Cockshull (1971) found that delivering a constant light intensity for 8 h or gradually increasing the light intensity up to a midday high then back down during an 8 h photoperiod did not influence the growth or development of chrysanthemum. However, Kinet (1977) found that the inflorescences of tomatoes developed properly when the plants were grown under an 8 h photoperiod and an irradiance of 1800 erg cm^{-2} s^{-1} (2.4 mol m^{-2} d^{-1}), while the inflorescences nearly all aborted when the plants were grown under a 16 h photoperiod and an irradiance of 900 ergs cm^{-2} s^{-1} (2.4 mol m^{-2} d^{-1}).

Experiments have shown that young leaves can inhibit flowering. A day neutral variety of tobacco remained vegetative when grown at 46 μmol m^{-2} s^{-1}, but flowered at a lower PPF (28 μmol m^{-2} s^{-1}) when young leaves were removed (Wardell, 1976). The

two youngest leaves of tomatoes grown at 25C utilized a much higher proportion of the available assimilates than plants grown at 15C; therefore, at higher temperatures the young leaves more strongly compete for assimilates (Hussey, 1962). It has been proposed that flower bud abortion in tomatoes is due to the competition for available photosynthates between vegetative and reproductive development (Calvert, 1969). The mobilization of leaf carbohydrates appears to be the mechanism for the effect of irradiance on flowering (Bodson et al., 1977).

Steffen et al. (1988) showed that sink activity and development rate were unchanged between flowers which had been covered during the entire inductive photoperiod versus uncovered flowers. Similar experiments with other species, e.g. roses (Zeislin and Halevy, 1975) resulted in flower abortion, indicating that irradiance affects more than photosynthesis.

PPF can modify the photoperiodic response of some plants. For example, high irradiance under SD conditions (96 W m^{-2}, full spectrum, for 8 h, or 11.4 mol m^{-2} d^{-1}) can eliminate the LD requirement for flowering in *Sinapsis* (Bodson et al., 1977). Bodson (1983) observed that the rate of flower development from flower initiation to the presence of ovules in the ovary of azaleas was increased as photoperiod was increased from 8 to 16 hours and also as PPF was increased from 80 to 160 μmol m^{-2} s^{-1}. Flower bud abortion did not occur when plants were grown at 255 μmol m^{-2} s^{-1} for 8 h (7.3 mol m^{-2} d^{-1}); however, 4 to 35% of the flower buds aborted on plants grown at 170 to 85 μmol m^{-2} s^{-1} for 8 h, respectively (4.8 and 2.5 mol m^{-2} d^{-1}). A night interruption which delivered 1.5 h of incandescent light at 15 μmol m^{-2} s^{-1} eliminated the occurrence of flower bud abortion regardless of the integrated PPF.

Temperature and Irradiance. Temperature can influence the critical photoperiod required for flowering. Chrysanthemum 'Encore' , a short day plant (SDP), required a shorter night length for flower initiation and a longer night length for flower development as night temperature was increased from 10 to 27C (Cathey, 1957). Lang (1965) observed that shorter night periods were required for the long day plant (LDP) *Hyoscyamus* as night temperature increased.

As temperature decreased from 24 to 15C the effect of SD on the SDP *Begonia x chiemantha* was reduced (Figure 8). The LD treatment can be completely replaced by low temperature treatments in the LDP *Silene* (Wellensiek, 1969) and SDP *Perilla* (Zeevaart, 1969). Temperatures above 30C can replace the requirement for LD in the LDP *Rudbeckia* (Murneek, 1948).

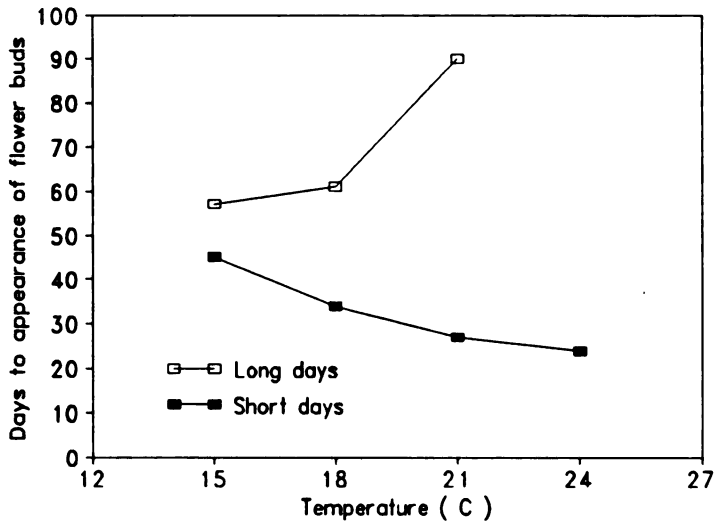

Figure 8. The interaction of temperature and photoperiod on flower development of *Begonia x chiemantha* (Heide, 1969).

Armitage et al. (1981) observed that as temperature increased from 10 to 27C, the light saturation point for geraniums increased from 700 to 1000 μmol m^{-2} s^{-1}. As temperature increased from 10 to 32C, the light compensation point increased from 25 to 75 μmol m^{-2} s^{-1}, and dark respiration increased from 2.7 to 9.0 mg CO_2 dm^{-2} h^{-1}.

The combination of a low irradiance and high temperature environment is often associated with flower bud abortion in Easter lily (Mastalerz, 1965). When natural irradiance is low during winter months, low temperatures are more effective at producing greenhouse crops. Low temperatures increase the duration of crop production time, thus allowing for more efficient usage of the low photosynthate supply (Harris and Scott, 1969).

Flower bud abortion did not occur on iris grown at 18C and 40 W m^{-2} for 16 h (10.6 mol m^{-2} d^{-1}), while 100% flower bud abortion occurred on plants grown at 18C and 40 W m^{-2} for 8 h (5.4 mol m^{-2} d^{-1}). Abortion did not occur at 40 W m^{-2} for 8 h (5.4 mol m^{-2} d^{-1}) when plants were grown at 12C yet increasing the temperature to 15C resulted in 88% abortion. Iris flower buds were also reported to be most sensitive to high temperature and low light conditions during the period of rapid elongation i.e. when the bud was first visible (Fortanier and Zevenbergen, 1973)

Modeling Plant Development

Degree-day models. A quantitative model is created by fitting a linear or a nonlinear function to data by means of regression analysis. The first models used to predict crop phenology were degree-day models (Bomalaski 1948). Degree-day models describe rate of development as a linear function of temperature (Figure 9). The base

temperature (T_{Base}), is the threshold temperature at which development begins to occur. Daily maximum (T_{Max}) and minimum (T_{Min}) temperatures are often used in calculating degree-day. Eq. 1 can be used to calculate the number of degree-days accumulated over a given day using T_{Min}, T_{Max}, and T_{Base}.

$$\text{Degree-days} = (T_{Max} - T_{Min})/2 - T_{Base} \quad (1)$$

Summation of degree-days required for a developmental process to occur gives a measure of the thermal time, or heat units, required for a stage of development to occur. Heat units have been used to predict budbreak in woody species (Eisensmith et al, 1980) and to predict harvest dates of many crops including blueberries (Carlson and Hancock, 1991), pecans (Sparks, 1989), and cucumbers (Perry and Wehner, 1990).

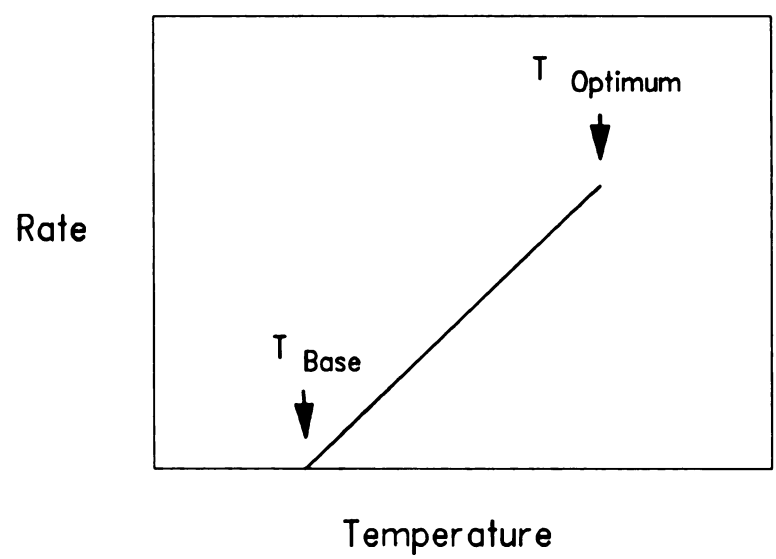

Figure 9. A degree-day model relating rate of development as a linear function of temperature.

Development rate can be described by the reciprocal of the time (T) required for the particular stage of development.

$$\text{Development rate} = 1/T \qquad (2)$$

The degree-day model has improved the accuracy with which development can be predicted as compared to using chronological time (Gallegher et al., 1979; and Kirby and Perry, 1987); however, there are problems associated with its use (Wang, 1960). The major error in the degree-day model is that the predicted developmental response to temperature is linear, while the actual developmental response to temperature is curvilinear when a sufficiently wide range of temperatures are examined.

Many alternative formulations of Eq. 1 have been developed to improve the degree-day model's accuracy at the high and low temperature extremes (Figure 10).

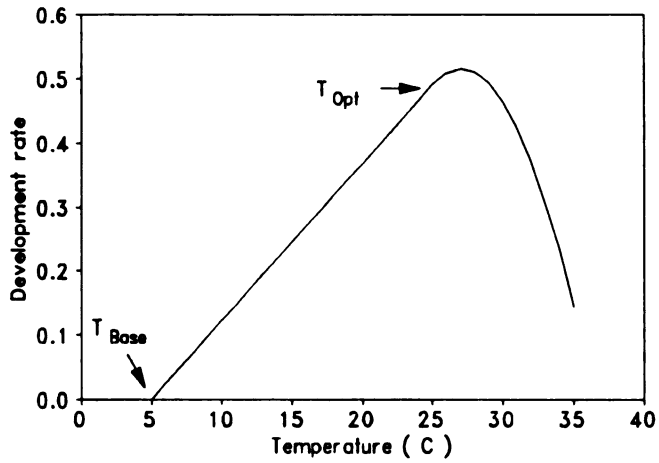

Figure 10. Degree-day model which compensates for reduced development rate at supraoptimal temperatures (Cross and Zuber, 1972).

Eq. 3 provides an example of a degree-day model which accounts for temperatures outside the linear range. The rate of development is calculated to be zero when the temperature is less than T_{Base}. A linear function is calculated when the temperature is between T_{Base} and T_{Opt}. A quadratic function is used to calculate rate of development at temperatures above T_{Opt}:

$$\begin{aligned} T \leq T_{Min} \quad &: DD = 0 \\ T_{Min} < T \leq T_{Max} \quad &: DD = a(T - T_{Min}) \\ T > T_{Max} \quad &: DD = b(T_{Max} - T_{Min})^2 \end{aligned} \tag{3}$$

where DD represents the number of degree-days.

A sine wave can be generated from the daily minimum and maximum temperatures and used to calculate the accumulated heat units. Baskerville and Emin (1969) described several methods for using a sine curve to generate values for the daily heat units accumulated. Figure 11 depicts four methods of calculating accumulated heat units.

Polynomial models. A cubic linear function can be used to represent the biological response of a plant over a wide range of temperatures. Figure 12 shows a cubic function used to predict the LAR of *Hibiscus* as a function of temperature. Polynomial functions have been used to describe the rate of development in the Easter lily (Erwin and Heins, 1990), beans (Yourstone and Wallace, 1990), and maize (Tollenaar et al., 1979). The advantage of using polynomial functions is the relative ease with which these models can be generated. The disadvantage is that polynomial

expressions, e.g. temperature^2, temperature^3, and temperature * photoperiod^2, seldom have any biological significance.

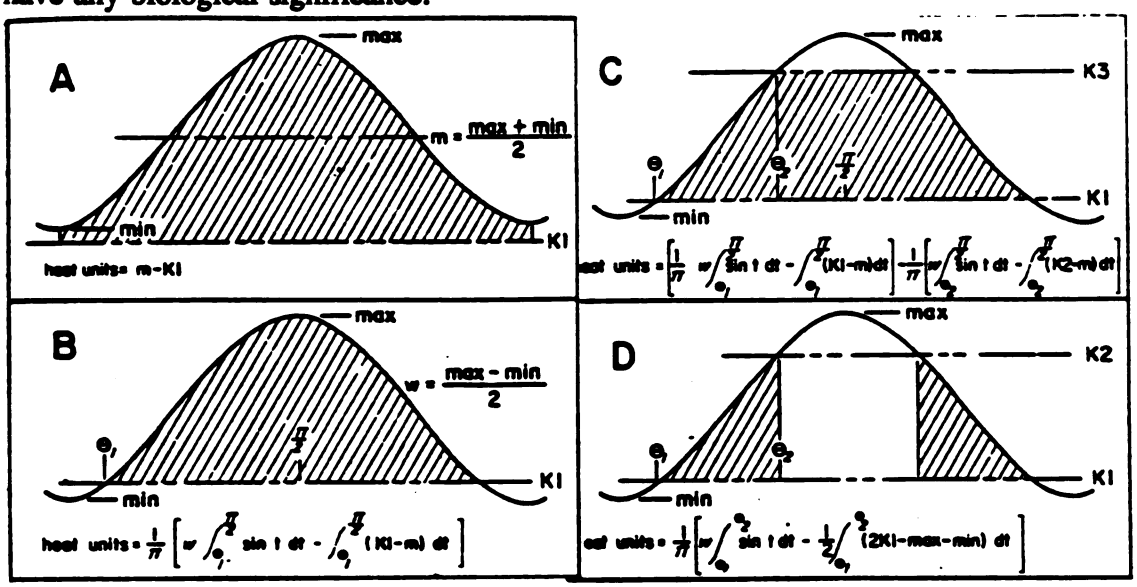

Figure 11. Four methods of calculating the accumulated heat units by means of a sine curve. In each case, the horizontal axis represents 24 hours, the vertical axis represents temperature, and the hatched area represents the accumulated heat units (Baskerville and Emin, 1989). A) The daily minimum temperature is above the lower threshold (K1), and there is no upper threshold. B) The daily minimum is below the lower threshold (K1) and there is no upper threshold. C) No restriction on the daily minimum, the daily maximum exceeds the upper threshold (K3), there is no cutoff at the upper threshold. D) No restriction on daily minimum, daily maximum exceeds upper threshold (K2), vertical cutoff at the upper threshold.

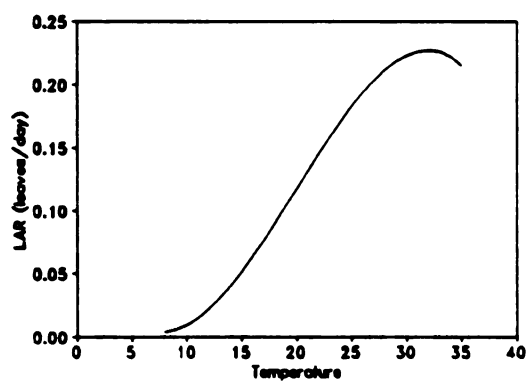

Figure 12. Polynomial function (Y = 0.089 - 0.0237 * Temp. + 0.00189 * Temp.^{2} - 0.00003177 * Temp.^{3}) describing the LAR of *Hibiscus* as a function of temperature (Karlsson et al., 1991)

Nonlinear models. Nonlinear functions have been used to describe the time from emergence to tassel initiation of maize (Coligado and Brown, 1975), and LAR and flowering in spring wheat (Angus et al., 1981). Nonlinear models can contain biologically significant variables. For example, the functions in Eq. 4 can be used to describe a developmental response to temperature (Reed et al., 1976).

$$Y=F(T)=a(T-T_{Min})(T_{Max}-T)^{b}$$
$$a=Y_{Max}/(T_{Opt}-T_{Min})(T_{Max}-T_{Opt})^{b} \qquad (4)$$
$$b=(T_{Max}-T_{Opt})/(T_{Opt}-T_{Min})$$

The parameters in this function, T_{Min}, T_{Max}, T_{Opt}, and Y_{Max}, all have biological significance. An example of Eq. 4 is provided in Figure 13.

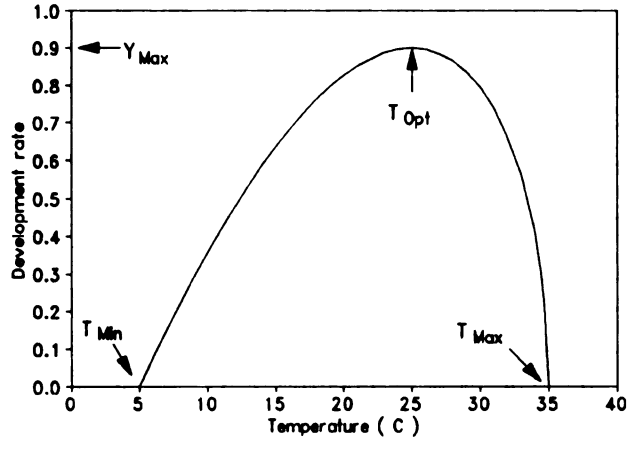

Figure 13. Nonlinear model used to describe rate of development based on four biologically significant parameters, T_{Min}, T_{Opt}, T_{Max}, and Y_{Max} (Reed et al., 1976).

Nonlinear models can be combined to predict the effect of two or more variables on development. The nonlinear model shown in Eq. 5 was used to predict the developmental response of maize to temperature and photoperiod.

$$\text{Rate of development} = 1/\text{Time}_{Opt}*(F_1(\text{Temperature})*F_2(\text{Photoperiod})) \quad (5)$$

Time_{Opt} refers to the time required for a developmental phase to be completed under optimal conditions. Time_{Opt} can have unique value for different cultivars (Coligado and Brown, 1975) or groupings of cultivars (Kiniry et al., 1991). F_1(Temperature) and F_2(Photoperiod) are nonlinear exponential models.

$$F_1(\text{Temperature}) = 1\text{-EXP}(-\beta(T-\tau)) \quad (6)$$

$$F_2(\text{Photoperiod}) = 1\text{-EXP}(-\sigma(L-\Gamma)) \quad (7)$$

τ and Γ are parameter estimates for the base temperature and critical photoperiod, respectively. β and σ are the parameter estimates for the temperature and photoperiod coefficients, respectively. Whenever the environment is at the optimal temperature and photoperiod for development, the values of the nonlinear model will be equal to 1; thus, the development rate will be optimized. If either temperature or photoperiod deviate from the optimal conditions, then a positive value less than 1 is calculated, and the rate of development will decrease. Finally, if either temperature or light are below the threshold values, the model will be equal to 0, then no development will be predicted (Figure 14).

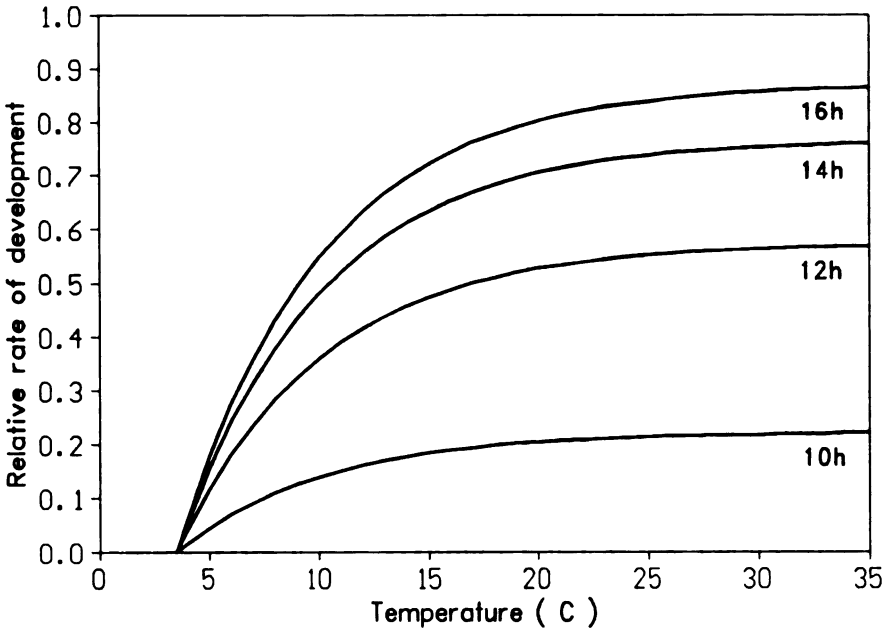

Figure 14. A nonlinear model (Eqs. 5 & 6) describing the interaction of temperature and photoperiod on the relative rate of development (Coligado and Brown, 1975).

The choice of variables to include in the model depends upon the phenological stage and the species examined. Table 4 shows the environmental variables used in a model for different stages of soybean development (Hodges and French, 1985).

Analysis of fluctuating temperature data. Results from experiments which contain treatments with different temperatures can be difficult to analyze, especially when the temperatures fall outside the linear range. For example, plants grown in a 30C day temperature and 10C night temperature would develop at a slower rate than plants grown at the same ADT of 20C. McNaughton et al.(1985) proposed a method of evaluating data from changing temperature treatments. Multiple linear regression analysis was used to create a model which describes the observed rate of development as a function of the fraction of time (T_1 to T_4) spent at each temperature (Table 5). Eq. 8 calculates the

Table 4. Variables used to predict development during different stages of soybean development (Hodges and French, 1985).

Stage	Variables
Emergence	Temperature, water stress
Juvenile	Temperature, water stress
Photoperiod-sensitive	Photoperiod
Floral growth	Temp., water stress, photoperiod
Flowering	Temp., water stress, photoperiod
First pod growth	Temp., water stress, photoperiod
Last pod growth	Temp., water stress, photoperiod

predicted rate of development under the mixed temperature treatments. The coefficients in Eq. 8 (b_1 to b_n) reflect the expected rate of development had plants been grown at constant temperatures.

$$Y=r(T)=b_0+b_1*T_1+\ldots b_n*T_n \qquad (8)$$

where the intercept $b_0=0$, and the coefficients, b_1, $b_2 \ldots b_n$ represent the predicted rates of development at 15, 20, 25, and 30C respectively.

Table 5. The rates of development from sowing to flower initiation for seven treatments. Columns T_1 to T_5 represent the percentage of time each treatment received the indicated temperature (McPherson et al., 1985)

Temperature (C)					Rate of development
16	20	24	26	30	
T_1	T_2	T_3	T_4	T_5	
0.5	0	0.5	0	0	0.021
0	0.5	0.5	0	0	0.025
0	0.5	0	0.5	0	0.024
0	0	0.5	0.5	0	0.025
0	0	0.5	0	0.5	0.020
0	0	1.0	0	0	0.026
0	0	0	1.0	0	0.024

Figure 15 shows the same data plotted as a function of average daily temperature, while Figure 16 shows the rates of development from Table 5 as predicted by McNaughton's method.

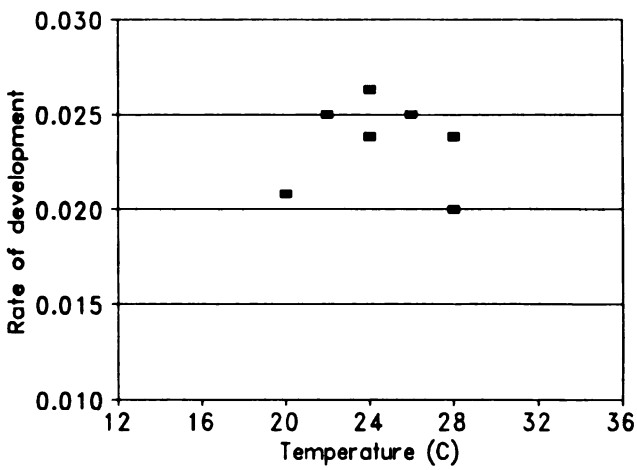

Figure 15. Observed mean rates of development from sowing to flower initiation of Pigeonpea plotted against mean temperature for each treatment (McPherson et al., 1985).

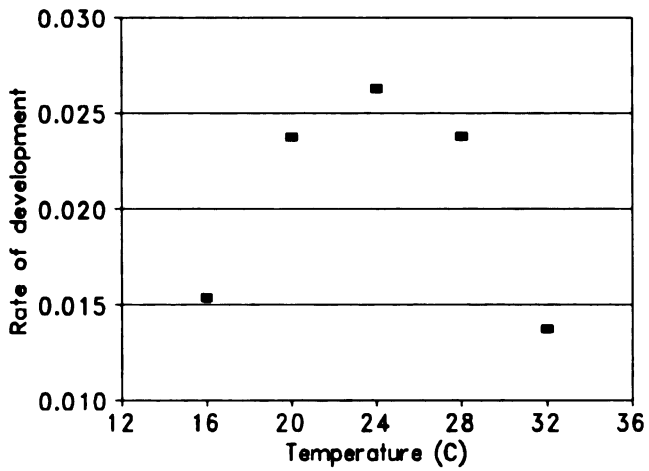

Figure 16. Fractional rates of development from sowing to flower initiation of Pigeonpea (McPherson et al., 1985).

Plastichron index. Another method developed to quantify the developmental status of plants is the plastichron index (PI). PI can be defined as the interval of time occurring between the stages of development of successive events such as leaf development. A method of determining fractional PI's is illustrated in Figure 17. The lines labeled n and n+1 represent the rate of elongation of successive leaves. The line AC represents the leaf length which serves as a reference length (L_{Ref}) used for comparison of leaf development. The line DE represents a specific point in time. Assuming that n and n+1 are parallel and AC and DE are perpendicular, then DB/BE = AB/BC. The length of leaves n and n+1 can be measured, and the plastichron age of the plant are calculated with the following formula:

$$PI = n+(\ln(L_n)-\ln(L_{Ref}))/(\ln(L_n)-\ln(L_{n+1}) \quad (9)$$

where n is the number of leaves longer than the reference length, and L_n is the length of the leaf n.

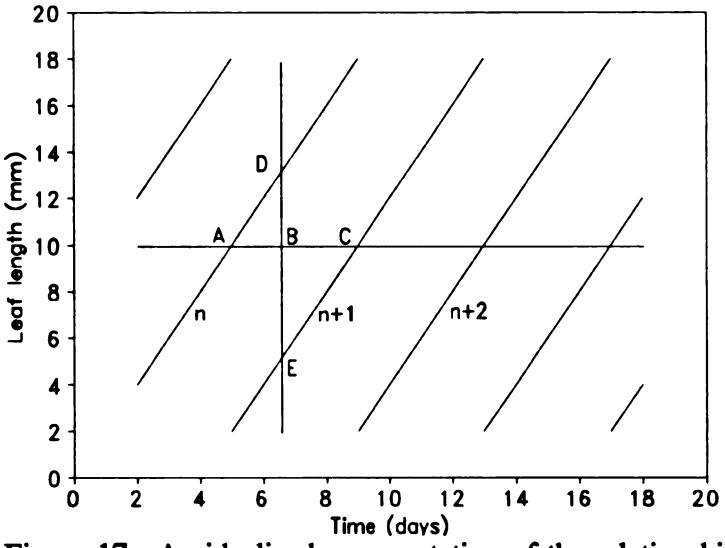

Figure 17. An idealized representation of the relationship between leaf length and time for a single shoot (Lamoreaux et al., 1978).

PI gives a quantitative measurement of the development which has occurred within a stage. For example, a plant can be described as being at the 3.4 plastichron interval; therefore, the relative progress between the third and the fourth leaf stage is quantified.

PI has been used to model plant development (Hofstra et al., 1977) as well as to evaluate environmental effects on plant development (Snyder and Bunce, 1983). However, assumptions must be made that the logarithmic growth curves of successive developmental stages are linear, parallel and equally spaced. These three assumptions can usually be made under the constant conditions of a controlled-environment study, but

not in the fluctuating environment in greenhouse or field studies (Yourstone and Wallace, 1990).

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SECTION I

MODELING LEAF DEVELOPMENT OF THE AFRICAN VIOLET (*Saintpaulia ionantha* WENDL.)

Modeling Leaf Development of the African Violet (*Saintpaulia ionantha* Wendl.)

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Production and Culture

Modeling Leaf Development of the African Violet (*Saintpaulia ionantha* Wendl.)

Additional index words. daily integrated photosynthetic photon flux density, irradiance, nonlinear function, temperature

Abbreviations: LUR, Leaf unfolding rate; PPF, Photosynthetic photon flux density

Abstract. The rate of leaf unfolding was determined for African violet (*Saintpaulia ionantha* Wendl.) 'Utah' plants grown under 20 combinations of temperature and PPF. A nonlinear model was used to predict LUR as a function of temperature and daily integrated PPF. The minimum and maximum temperatures for leaf unfolding were estimated at 8 and 30.8C, respectively. The maximum predicted LUR was 0.266 leaves day^{-1} which occurred at 25C and a daily integrated PPF of 10 mol m^{-2} d^{-1}. The optimum temperature for leaf unfolding decreased to 23C and the maximum rate decreased to 0.175 leaves day^{-1} as the daily integrated PPF decreased from 10 to 1 mol m^{-2} d^{-1}. A greenhouse validation experiment using 12 combinations of temperature and daily integrated PPF was conducted to validate the LUR model. Plant temperature was measured by inserting a hypodermic-needle thermocouple probe into the stem near the apical meristem. Plant temperatures used in the model predicted leaf development more accurately than did air temperatures, but using average hourly temperature data was no more accurate than using average daily temperature data.

Saintpaulia ionantha Wendl., commonly referred to as the African violet, is an important greenhouse crop in the United States. In 1990, 23 million pots were sold at a wholesale value of 27.6 million dollars (Anonymous, 1990). Production occurs year around in the United States and peaks at holidays; Valentine's Day is the largest marketing date. Most commercial producers of African violets begin production by purchasing small plants or "plugs" which usually possess 8 to 12 unfolded leaves. The plugs are transplanted into 10 cm diameter pots, grown, and then sold when the plants have approximately 20 to 25 unfolded leaves and five or more open flowers.

Phasic development scales have been used to identify the status of phenological development. Vegetative development can be described by leaf number and the rate at which leaves appear, or unfold. Phenological scales can be useful to the grower for identifying both the current developmental status of a crop, and the development required over a future period of time in order for a crop to be at the proper stage of development at the market date.

Temperature is the primary variable used in models to predict rates of development (Hodges, 1991). Average hourly temperatures (Karlsson et al., 1991), average daily temperatures (Karlsson et al., 1988), and minimum and maximum daily temperature (Hodges and French, 1985) data have been used in plant-development models. Air temperatures are most commonly used in leaf-development models; however, soil temperatures have also been used to predict development of species such as wheat while the apical meristem is below the soil surface (Swan et al., 1987).

PPF is a variable which is not usually included in leaf-development models; however, Hanchey (1955) observed that leaf number of African violets decreased from

44 to 22 leaves per plant as illuminance decreased from 600 to 100 footcandles for 6 h per day (1.9 to 0.31 mol m^{-2} d^{-1}). The African violet is a shade plant (Johansson, 1978); therefore, commercial producers grow African violets under shadecloth. Also, the daily integrated PPF delivered to a crop during cloudy, winter conditions can be below 2 mol m^{-2} d^{-1}.

Both temperature and PPF influence development rate of the African violet and can be computer controlled and monitored in greenhouse environments; therefore, temperature and PPF need to be considered in the development of African violet phenology models.

The objectives of our research were twofold: first, to describe the influence of temperature and PPF on the rate of leaf development of the African violet and second, to develop a model which would predict leaf development in the greenhouse environment.

Materials and Methods

Model description. LUR, expressed in the number of leaves unfolded per day, describes the rate at which leaves unfold, or appear, at the apical meristem. A leaf was considered unfolded when the leaf blade reached 7 mm in length. The slope of a linear regression line fit to the number of unfolded leaves as a function of time represented the LUR for a given plant.

The following nonlinear functions (Reed et al., 1976; Landsberg, 1977) were used to describe LUR as a function of both temperature and daily integrated PPF:

$$LUR = A(T-T_{Min})(T_{Max}-T)^{B} \quad (1)$$

$$A = LUR_{Max}/(T_{Opt}-T_{Min})(T_{Max}-T_{Opt})^{B} \quad (2)$$

$$B = (T_{Max}-T_{Opt})/(T_{Opt}-T_{Min}) \quad (3)$$

where T_{Min} and T_{Max} refer to the minimum temperature and the maximum temperature at which LUR is zero. T_{Opt} is the temperature at which the optimum LUR occurs for a given daily integrated PPF. LUR_{Max} refers to the maximum value for LUR at a given daily integrated PPF. The following nonlinear functions were used to describe LUR_{Max} and T_{Opt}:

$$T_{Opt} = a_0+a_1*EXP(a_2*PPF_{DI}) \quad (4)$$

$$LUR_{Max} = b_0+b_1*EXP(b_2*PPF_{DI}) \quad (5)$$

where a_0 and b_0 indicate the asymptotic values of the functions, and a_1, a_2, b_1, and b_2, are parameter estimates.

Estimating parameters. Parameter estimates and asymptotic 95% confidence limits (Table 1) for the nonlinear functions were estimated with SAS procedure NLIN (SAS Institute, Inc., 1989). In previous experiments the minimum temperature for leaf growth of the African violet was approximately 8C (Faust and Heins, unpublished data); therefore, the value of T_{Min} was fixed at 8C.

Experimental design. A split plot design was used with temperature as the main plot and PPF as the split plot. Four PPF treatments were located in each of five temperature treatments. Five plants were grown in each of the 20 temperature/PPF

treatments. African violet 'Utah' plants possessing 8 to 10 unfolded leaves were received in 3 cm diameter (22 cm^3) cells and transplanted into 10 cm diameter pots (450 cm^3) containing a commercial peat-based medium (Baccto Professional Plant Mix, Michigan Peat Co., Houston, TX). Immediately after transplanting, plants were placed into one of five (6.3 m^2) walk-in growth chambers (Hotpack, Model UWP 3009-2, Philadelphia, PA). Air temperature was adjusted to maintain plant temperatures at 14, 18, 22, 26, and 30C. Plant temperature was measured by inserting a hypodermic-needle thermocouple probe (Omega Hyp1-30-1/2-T-G-60-SMP-M) into stem, petiole, and leaf tissue. Layers of neutral-density shadecloth were placed above the plants in each growth chamber to create PPF of 23, 92, 161, 230 μmol m^{-2} s^{-1}. PPF was supplied 12 h per day by cool white fluorescent lamps (Philips VHO F96T12/CW/VHO) which resulted in daily integrated PPF treatments of 1, 4, 7, and 10 mol m^{-2} day^{-1}. The range of PPF treatments delivered within a chamber resulted in a $\pm$1C plant-temperature difference between PPF treatments.

Dates of leaf unfolding were recorded every 2 to 4 days until the first flower had opened on each plant or until day 77 of the experiment. Orthogonal polynomial contrasts were utilized to determine the trend analyses. SAS procedure GLM (General Linear Models) (SAS Institute Inc., 1989) was used for analysis of variance.

Greenhouse validation of the LUR model. Four 10 m^2 glass greenhouses were set to maintain air temperatures of 15, 20, 25, or 30C from December, 1990, to February, 1991. Greenhouse temperatures were controlled by a greenhouse climate-control computer (Priva, Model CD750, De Lier, Holland). Each greenhouse was divided into thirds to provide three PPF treatments. Plants in the low-PPF treatment

were placed under neutral-density shadecloth to reduce natural PPF by 50%. Plants in the medium-PPF treatment received the natural-PPF environment. From 0600 to 1800 h each day (4.3 mol m^{-2} d^{-1}), plants in the high-PPF treatment received natural PPF plus an additional PPF of 100 μmol m^{-2} s^{-1} supplied by 400 W high-pressure sodium lamps (Phillips Electronics Ltd., Model SGH701, Ontario, Canada). Another layer of 50% PPF-reduction neutral-density shadecloth was pulled over all PPF treatments when the natural PPF increased above approximately 300 μmol m^{-2} s^{-1}. The average daily integrated PPF were 2.6, 4.5, and 8.8 mol m^{-2} d^{-1} for the three PPF treatments over the course of the experiment.

PPF was monitored at canopy level with LI-COR (LI-1909A) quantum sensors. Plant temperature in each treatment was monitored by inserting hypodermic-needle thermocouple probes (Omega Hyp1-30-1/2-T-G-60-SMP-M) into the stem near the apical meristem. Thirty-minute average plant temperatures and PPF measurements were recorded with a datalogger (Easy Logger 800, Omnidata International, Logan, Utah,). Air temperature was monitored 30 cm above the canopy with a shaded and aspirated thermocouple. Two hour average air temperatures were also recorded with a datalogger (Digistrip III, Kaye Instruments Co., New Bedford, Conn.).

All plants were subirrigated with a nutrient solution consisting of 3.6 mmol N and 1.3 mmol K from calcium and potassium nitrate or watered based upon the electrical conductivity of the medium. Electrical conductivity of the media in the root zone was maintained between 0.5 and 1.0 mS throughout the experiment using the 2:1 water/soil (vol/vol) method (Warncke and Krauskopf, 1983). The electrical conductivity of the irrigation water was 0.65 mS and the bicarbonate alkalinity was 310 mg l^{-1}.

0.25 to 0.5 ml phosphoric acid per liter irrigation water was applied to the medium as needed to maintain media pH between 5.5 and 6.5.

Tests of model prediction. Four methods of averaging actual temperature data were compared when the LUR model was validated. The methods were based on 1) average hourly plant temperature, 2) average hourly air temperature, 3) average daily plant temperature and 4) average daily air temperature. The calculated average temperatures were used along with the daily integrated PPF to predict LUR on either an hourly or daily basis.

ADT was calculated from measurements taken from 0600 HR one day to 0600 HR the following day. Daily integrated PPF measured during the photoperiod of one day was used to calculate LUR starting at the beginning of the photoperiod of that same day and continuing for 24 h until the beginning of the next photoperiod. For example, daily integrated PPF measured from 0700 to 1700 HR on January 1 was used in the LUR model along with the average daily or hourly temperatures from 0700 HR on January 1 to 0600 HR of January 2 to calculate LUR from 0700 HR on January 1 to 0600 HR of January 2.

Two techniques were used to compare the predictive value of the four methods of using temperature data in the LUR model. First, the absolute deviation between actual and predicted leaf number was calculated for each recorded leaf number. Second, the slope of the observed leaf number plotted against the predicted leaf number was calculated by linear regression. Perfect prediction of the rate of leaf unfolding would result in a slope equal to one; therefore, the absolute deviation between the slope of the

predicted leaf number and the slope of the observed leaf number provided another comparison of the methods for entering temperature data into the LUR model.

Results

The leaves of each plant unfolded as a linear function of time (Figure 1). Temperature, daily integrated PPF, and the interaction between temperature and daily integrated PPF significantly influenced LUR (Table 1). LUR increased as temperature increased from 14C to an optimum temperature, and then decreased sharply as temperature increased above the optimum temperature. LUR also increased at all temperatures as daily integrated PPF increased from 1 to 7 mol m^{-2} d^{-1}, but did not increase further at 10 mol m^{-2} d^{-1} (Figure 2).

The statistically significant interaction between temperature and daily integrated PPF was reflected by the increase in T_{Opt} and LUR_{Max} as daily integrated PPF increased with respect to temperature. T_{Opt} increased from 22.6 to 25.5C (Figure 3A), and LUR_{Max} increased from 0.175 to 0.27 leaves d^{-1} (Figure 3B) as the daily integrated PPF increased from 1 to 10 mol m^{-2} d^{-1}.

A model was created which predicts LUR based on temperature and daily integrated PPF data (Figure 2). Estimates for the parameters in Equations 1-5 are shown in Table 2.

In the greenhouse-validation experiment, average hourly air temperatures were usually maintained within $\pm$1.5C of the setpoint temperature, while plant temperature frequently differed from air temperature. Plant temperature during the photoperiod was closely correlated to the instantaneous solar radiation. Plant temperature during the

daylight hours on cloudy days was often 1 to 3C below air temperatures (Figure 4A), while plant temperature during the daylight hours on sunny days was up to 3C higher than air temperature (Figure 4B). Plant temperature during the night was typically 2 to 5C lower than air temperature (Figure 4 A, B, & C). Plant temperature increased 3 to 4C when the high-pressure sodium lamps were used (Figure 4C).

Plant temperature data predicted leaf number more accurately than air temperature data based on a comparison between actual and predicted leaf numbers. The precision of the model was not improved by using average hourly temperatures rather than average daily temperatures (Table 3).

The leaf unfolding model (Eqs. 1-5) accurately predicted leaf unfolding over 77 days of the validation experiment (Figure 5). The predicted leaf number was within one leaf of the observed leaf number 84% of the time (more than 300 measurements on 48 plants) when average daily plant temperatures were used in the model (Figure 6).

Discussion

The influence of temperature on leaf development of African violets was similar to other plant species. In African violets, we determined T_{Min} to be 8C, T_{Opt} to be between 23 and 25.5C, and T_{Max} to be 30.8C, temperatures similar to those determined for other tropical species (Kiniry et al., 1991). LUR_{Max} varies considerably from 0.10 leaves day^{-1} for banana (Allen et al., 1988) to 2.5 leaves day^{-1} for the Easter lily (Karlsson et al., 1988). LUR_{Max} for African violets was 0.266 leaves day^{-1}.

Leaf development was influenced by daily integrated PPF. PPF is not typically used in plant development models because the daily integrated PPF at which most crops

are produced is sufficiently high to saturate the photosynthetic apparatus. However, African violets are susceptible to physiological damage at high PPF, so growers often produce African violets at PPF which can limit photosynthesis and leaf development. Therefore, daily integrated PPF was included as a variable in the LUR model.

No significant difference resulted from using average hourly temperatures in the model as compared to average daily temperatures. Similar results have been observed by researchers using degree day models (Cross and Zuber, 1972; Gilmore and Rogers, 1958). The temperature-response curves used in the LUR model were developed from data collected on plants grown at constant temperatures, but may not reflect the developmental responses which occur during brief exposures to temperatures outside the linear-response range. Therefore, the model reflects development rates which occur over broader time intervals; thus, average daily temperatures were the most accurate at predicting leaf development.

Plant temperatures gave a more accurate prediction of leaf number with the LUR model than air temperatures. The actual developing plant-tissue temperature must be determined to accurately predict specific organ or tissue development. Harris and Scott (1969) observed that independent fluctuations of plant-organ temperature, e.g., flower buds and leaves, determined the rate of their development.

Plant temperature is dependent on the energy exchange between the plant and its environment. During the night period of the greenhouse experiment, plant temperature was frequently 2 to 5C below air temperature. Part of this temperature difference can be attributed to energy loss to the greenhouse glass via long wave radiation (Hanan et al., 1978). However, we have also observed a 1 to 3C drop in temperature

of African violets during dark periods in growth chambers. Vogelezang (1988) also observed that meristem temperature of African violets is more closely correlated to soil temperature than to air temperature. We hypothesize that the observed difference between air and plant temperature is due at least in part to conductive heat transfer from the plant to the soil. The African violet has a rosette growth habit, and the meristem is typically less than 3 cm above the soil surface. Evaporation of water from the soil surface would result in evaporative cooling. Conductive heat transfer from the plant stem to the cooler soil would results in reduced plant temperatures.

In summary, an LUR model based on average daily plant temperatures and daily integrated PPF accurately predicted leaf development of African violets grown for 77 days in a greenhouse under a range of temperature and PPF conditions. Plant temperature predicted leaf development more precisely than did air temperature. No benefit was obtained by using average hourly temperatures rather than average daily temperatures.

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Figure 1. The rate of leaf unfolding for an African violet grown at 22C and a daily integrated PPF of 7 mol m^{-2} d^{-1} was 0.244 leaves d^{-1} as determined by the slope of the regression line $Y=0.244*X-0.302$ ($R^2=0.99$).

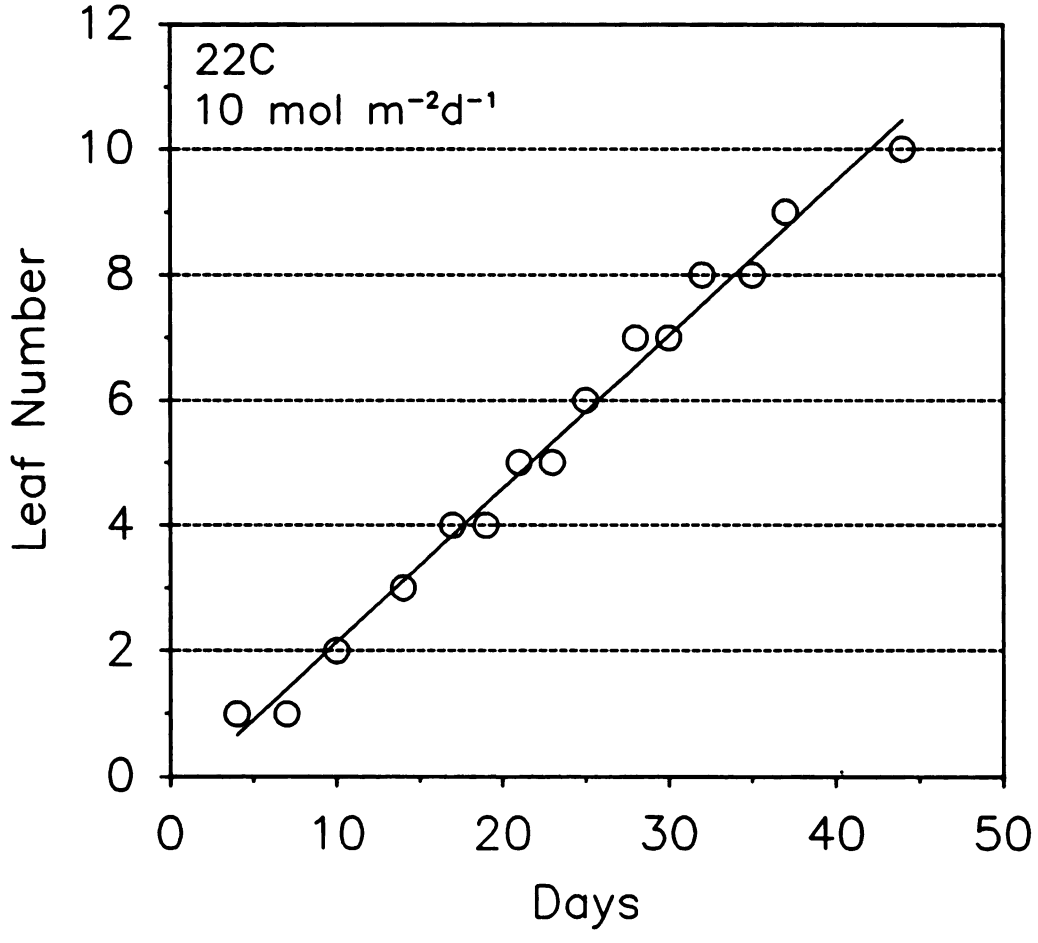
22C
10 mol m⁻²d⁻¹
Leaf Number
Days
0
2
4
6
8
10
12
0
10
20
30
40
50

Figure 2. Nonlinear model (Eqs. 1-5) describing LUR as a function of temperature and daily integrated PPF ($R^2=0.99$). Symbols represent treatment means.

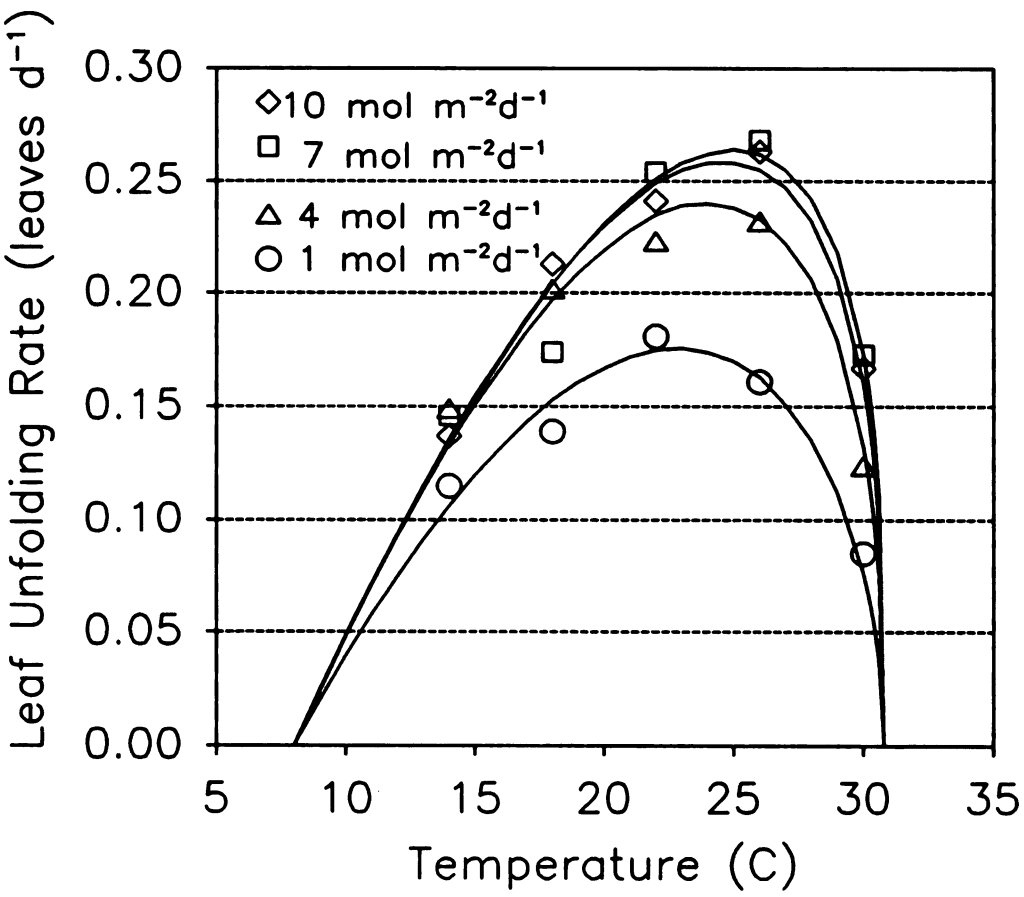
Leaf Unfolding Rate (leaves d-1)
0.30
0.25
0.20
0.15
0.10
0.05
0.00
10 mol m-2d-1
7 mol m-2d-1
4 mol m-2d-1
1 mol m-2d-1
5
10
15
20
25
30
35
Temperature (C)

Figure 3. The influence of daily integrated PPF on A) T_{Opt} (T_{Opt}=25.44-3.127* EXP(-0.193*PPF_{DI}))andB)LUR_{Max}(LUR_{Max}=0.266-0.137*EXP(-0.418* PPF_{DI})). Vertical bars indicate asymptotic 95% confidence intervals for T_{Opt} and LUR_{Max} values estimated at each daily integrated PPF treatment.

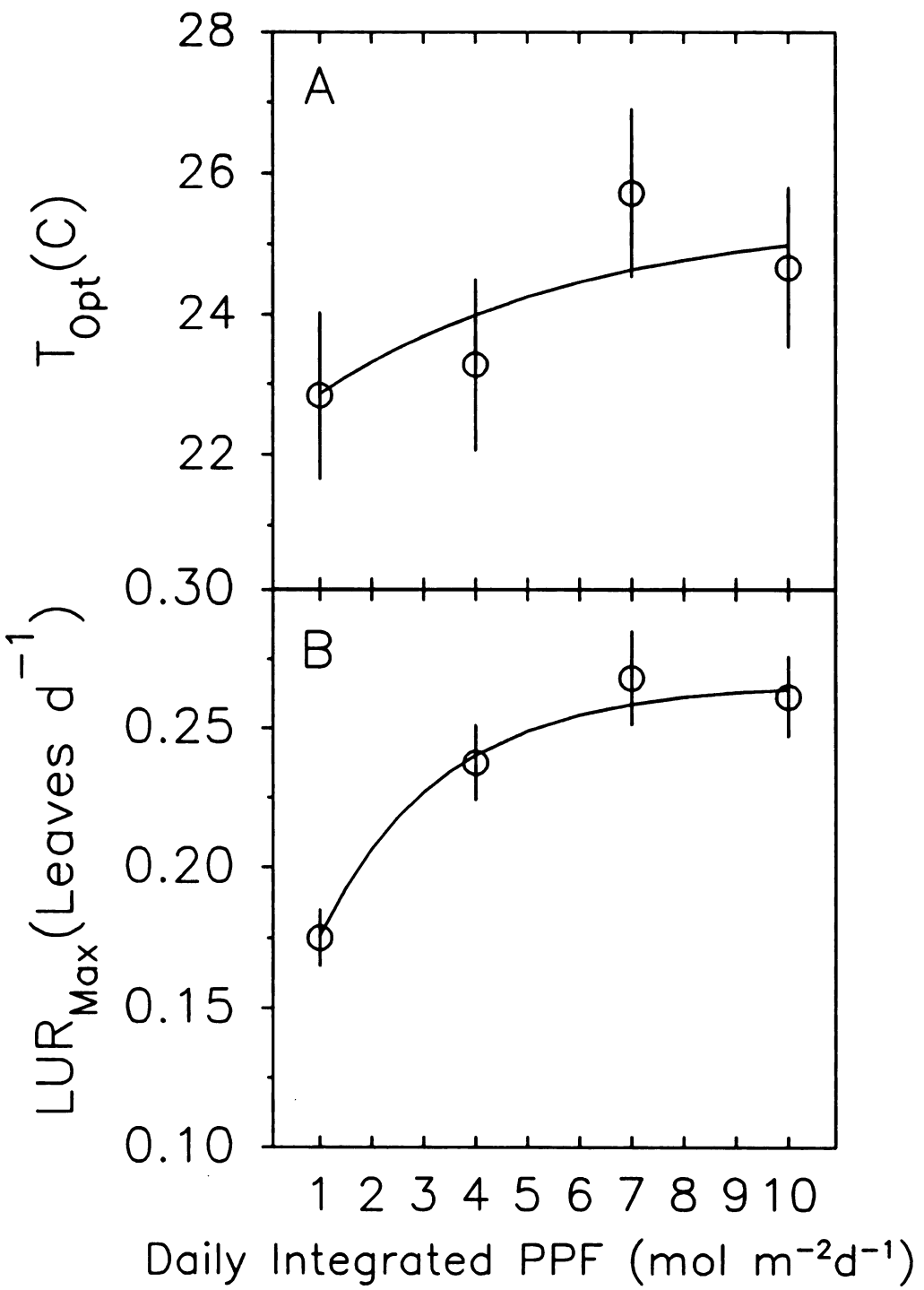
A
B
28
26
24
22
0.30
0.25
0.20
0.15
0.10
T_{Opt}(C)
LUR_{Max}(Leaves d^{-1})
1 2 3 4 5 6 7 8 9 10
Daily Integrated PPF (mol $m^{-2}d^{-1}$)

Figure 4. A comparison between air and plant temperature (A) over the course of a cloudy day (December 30, 1990), (B) a sunny day (January 3, 1991), and (C) a cloudy day in which the plants were growing under high-pressure sodium lamps from 0600 to 1800 HR (December 30, 1990).

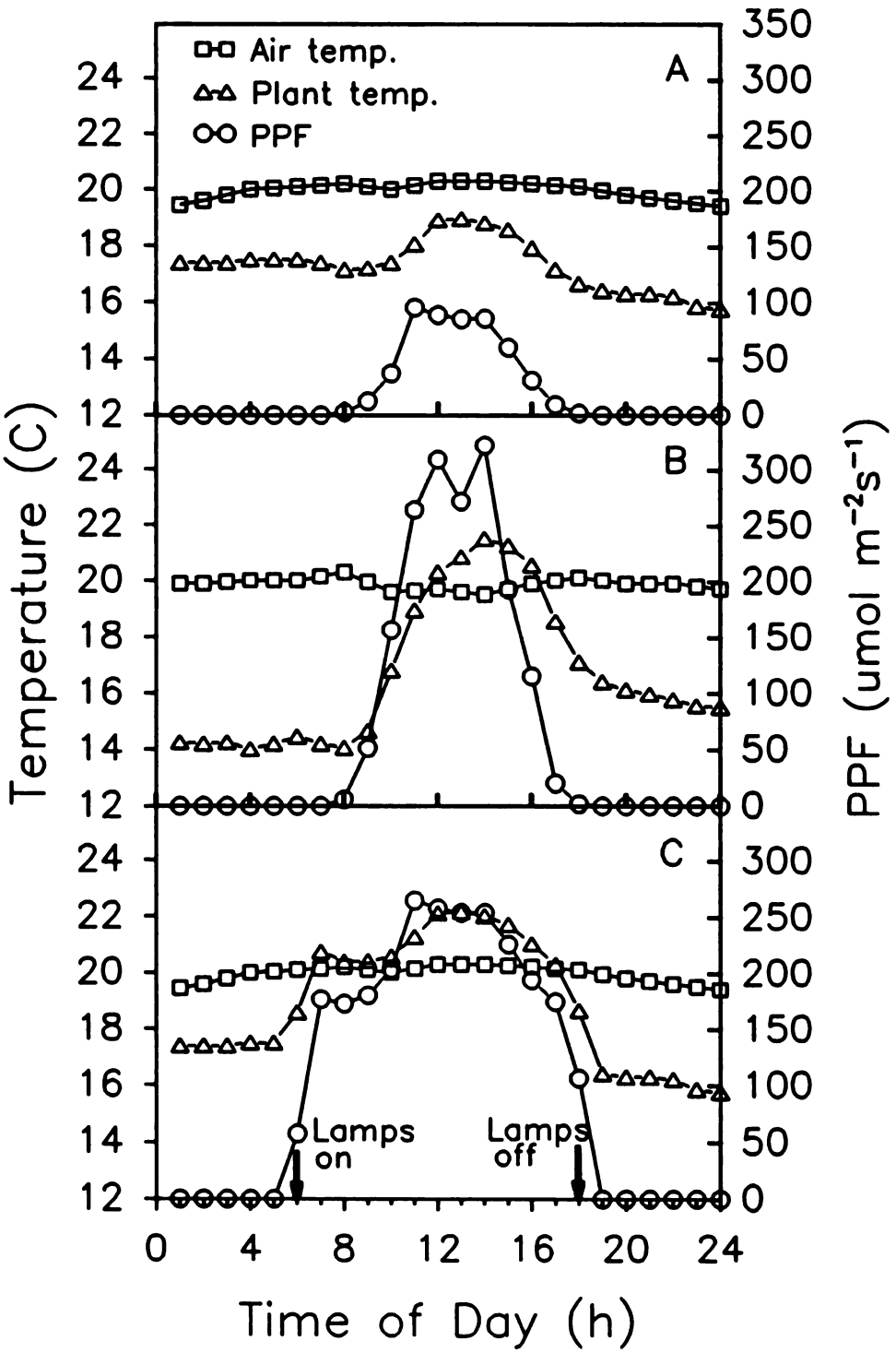
Air temp.
Plant temp.
PPF
A
B
C
Lamps on
Lamps off
Temperature (C)
PPF (umol m-2s-1)
Time of Day (h)
0
4
8
12
16
20
24
12
14
16
18
20
22
24
0
50
100
150
200
250
300
350

Figure 5. Comparison between the predicted (solid line) and observed (o) leaf number of plants grown in 12 temperature/PPF treatments.

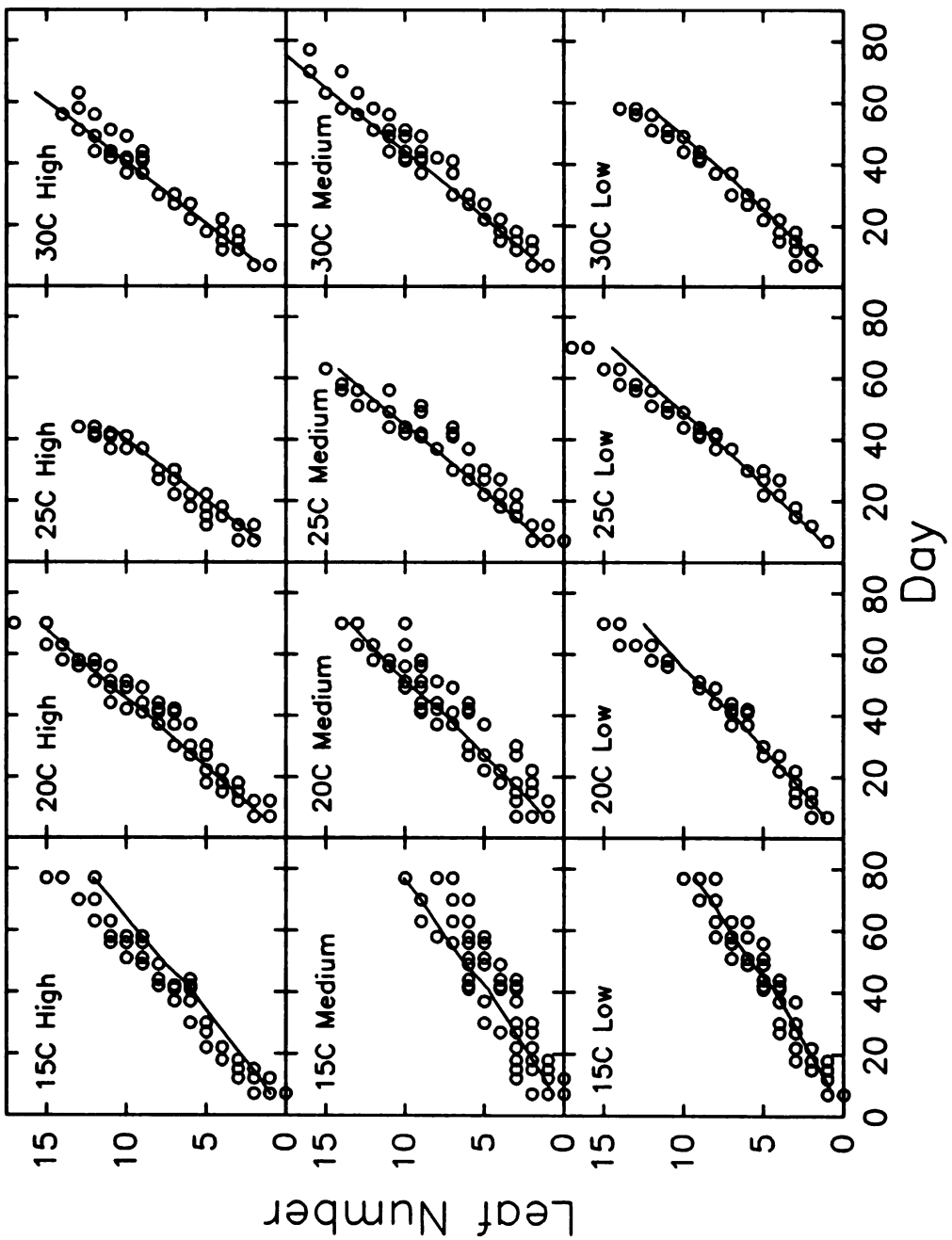
15C High
20C High
25C High
30C High
15C Medium
20C Medium
25C Medium
30C Medium
15C Low
20C Low
25C Low
30C Low
Leaf Number
Day
0
5
10
15
0
20
40
60
80

Figure 6. Comparison of the observed (o) and the predicted (solid line) leaf number of all of the plants in the 12 temperature and PPF treatments during the 77 days of the greenhouse-validation experiment.

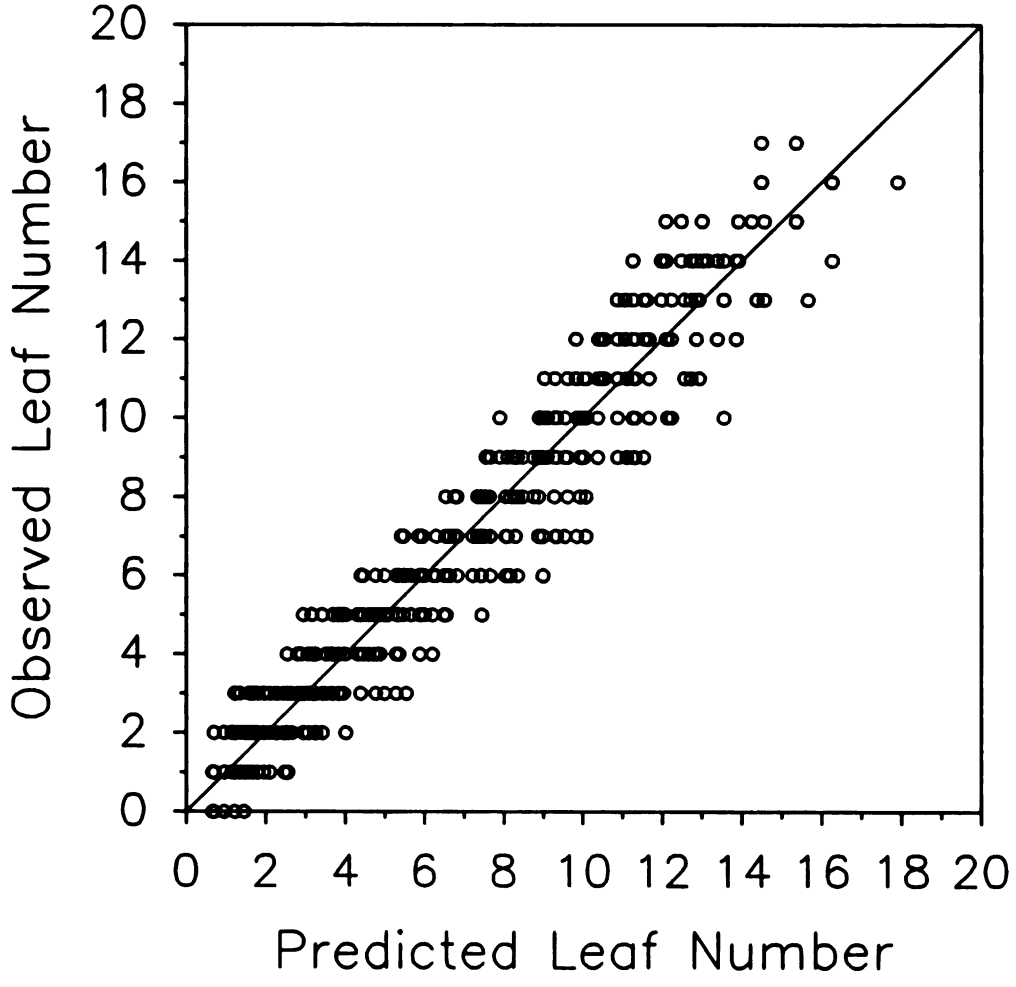
Observed Leaf Number
Predicted Leaf Number
0
2
4
6
8
10
12
14
16
18
20

Table 1. Influence of temperature and daily integrated PPF on LUR.

Temperature (C)	Daily integrated PPF (mol m^{-2} d^{-1})			
	1	4	7	10
	Leaf unfolding rate (leaves d^{-1})			
14	0.115	0.149	0.146	0.137
18	0.139	0.202	0.174	0.213
22	0.181	0.223	0.254	0.241
26	0.161	0.232	0.268	0.263
30	0.086	0.124	0.173	0.176

Source	Significance[z]
Temperature	
Linear	NS
Quadratic	***
Cubic	*
Daily integrated PPF	
Linear	***
Quadratic	***
Cubic	NS
Temp. x PPF_{DI}	***

[z] NS, *, *** Nonsignificant or significant at P=.05, .001, respectively.

Table 2. Parameter estimates and 95% confidence intervals calculated for use in the LUR model (Equations 1-5).

Parameter		Estimate	Asymptotic 95% confidence interval	
Equations 1, 2, & 3	Equations 4 & 5		Lower	Upper
T_{Max}		30.83	30.36	31.31
T_{Opt}				
	a_0	25.44	23.22	27.66
	a_1	-3.127	-4.861	-1.392
	a_2	-0.193	-0.559	0.173
Y_{Max}				
	b_0	0.266	0.252	0.280
	b_1	-0.137	-0.162	-0.112
	b_2	-0.418	-0.621	-0.215

Table 3. Comparison of four methods of using temperature data to predict leaf number.

Air Temp. (C)	Daily light integral (mol m^{-2} d^{-1})	Days to first flower	Mean leaf number at time of first flower[z]	Ave. hourly plant temp.	Ave. hourly air temp.	Ave. daily plant temp.	Ave. daily air temp.	Ave. hourly plant temp.	Ave. hourly air temp.	Ave. daily plant temp.	Ave. daily air temp.
				Deviation between predicted and observed leaf number (leaves)				Deviation between slopes of the predicted and the actual leaf numbers (leaves d^{-1})			
15	2.7	y	9.3	0.53	1.47	0.49	1.38	0.07	0.22	0.07	0.24
	4.8	y	8.3	0.94	2.22	1.07	2.13	0.16	0.35	0.21	0.36
	9.5	y	13.8	1.57	0.76	1.23	1.38	0.26	0.12	0.14	0.11
20	2.6	70	14.7	0.70	0.89	0.72	0.78	0.16	0.07	0.11	0.06
	4.6	70	12.8	0.92	1.40	0.95	1.32	0.07	0.18	0.11	0.20
	9.5	65	14.5	0.73	0.86	0.72	0.76	0.08	0.05	0.05	0.05
25	2.6	70	16.3	0.87	0.69	0.69	0.62	0.22	0.15	0.15	0.13
	4.6	60	13.8	0.93	1.06	0.84	0.90	0.15	0.08	0.10	0.08
	9.5	43	12	1.02	0.60	0.79	0.70	0.15	0.10	0.11	0.10
30	2.6	56	12.8	0.73	2.90	0.50	2.82	0.07	0.61	0.05	0.50
	4.5	63	14	0.67	2.09	0.85	1.81	0.05	0.37	0.07	0.28
	9.5	57	13.5	0.99	1.52	0.71	1.41	0.13	0.29	0.06	0.21
Mean				0.88 a	1.37 b	0.79 a	1.29 b	0.13 a	0.21 b	0.10 a	0.19 b

Mean separation by LSD, P=0.05.
[z] Leaf number was recorded on day 77 for plants which had not yet flowered.
[y] Plants not in flower after 77 days.

SECTION II

MODELING INFLORESCENCE DEVELOPMENT OF THE AFRICAN VIOLET (*Saintpaulia ionantha* WENDL.)

Modeling Inflorescence Development of the African violet (*Saintpaulia ionantha* Wendl.)

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Production and Culture.

Modeling Inflorescence Development of the African violet (*Saintpaulia ionantha* Wendl.)

Additional index words. leaf extension rate, photosynthetic photon flux density, temperature.

Abbreviations: ADT, average daily temperature; DT, day temperature; NT, night temperature; LER, leaf extension rate; LBL, leaf blade length; PPF, photosynthetic photon flux density; VB, visible flower bud

Abstract. The effects of temperature and PPF on flower initiation and development were quantified to provide a basis for an inflorescence development model. The percentage of leaf axils forming an inflorescence increased as the daily integrated PPF increased from 1 to 4 mol m^{-2} d^{-1}, while the rate of inflorescence development was a function of average daily temperature. The appearance of a visible bud in the leaf axil was correlated with leaf blade length of the subtending leaf. A polynomial function was used to describe leaf blade length at the time of visible bud as a function of temperature and daily integrated PPF. A nonlinear function was used to describe the influence of temperature on the rate of leaf extension. The time of visible appearance of an inflorescence in the leaf axil was then predicted by measuring the current leaf blade length and estimating the time required for the leaf blade to extend to the length required for VB appearance

The number of days required for an inflorescence to develop from visible bud to anthesis was influenced by temperature. A phasic development scale was used to describe the developmental status of an inflorescence. A model was then created which predicted time to anthesis based upon temperature and the current stage of inflorescence development. The number of days from the time of leaf unfolding to anthesis for the inflorescence which will be initiated in the leaf axil decreased from 87 to 57 days as temperature increased from 18 to 26C.

Commercial producers of container-grown flowering plants are required to produce plants for specific market dates; therefore, the ability to predict the date of anthesis for a crop is essential. Prediction requires the grower be able to identify the developmental status of a crop and then properly adjust the greenhouse environment so that the crop is flowering at the market date.

Accurate scheduling of African violet (*Saintpaulia ionantha* Wendl.) production for specific market dates can be very difficult for three reasons. First, the African violet is a day neutral species with respect to flower initiation and development (Halevy, 1985); therefore, the species does not possess a precise mechanism which can be used to induce flower initiation on a specific date. Second, the apical meristem grows indeterminately and inflorescences develop in leaf axils. Not all leaf axils produce an inflorescence and there is not a method available to determine which leaf axils will produce an inflorescence. Third, once initiation has occurred, quantitative data are not available relating the greenhouse environment to the rate of inflorescence development after initiation has occurred.

ADT is the primary factor influencing the rate of plant development (Hodges, 1991), not the relationship between DT and NT (Karlsson et al. 1988; Berghage, 1990). However, the literature conflicts on whether flower development of the African violet is a function of ADT or relationship between DT and NT. The African violet has been classified as a species which flowers faster when grown with cooler DT than NT (Leopold and Kriedemann, 1975; Kimmins, 1980; Mastalerz, 1965) based on data presented by Went (1957) which showed that African violets flowered more quickly when grown at 14C day temperature (DT) and 20C night temperature (NT) than when grown at constant 20C. However, Hildrum and Kristoffersen (1969) observed that time to flower, the number of flowers and buds per plant, inflorescences per plant, and flowers and buds per inflorescence were influenced by ADT, and not the relationship between DT and NT.

Initiation and development of an inflorescence in the leaf axil is influenced by the capacity of the leaves to export photosynthates . The transition from importing to exporting carbohydrates from a leaf is related to leaf expansion (Turgeon, 1989). As a result, flowering of some species is influenced by PPF (Kinet, 1977) and plant leaf area (Ramina et al., 1979). Likewise, a similar flowering response has been observed on African violet. Hildrum and Kristoffersen (1969) observed the number of flowers and buds per plant, inflorescences per plant, and flowers and buds per inflorescence increased as illuminance increased from 4 to 12 klux for 16 h (3.1 to 9.3 mol m^{-2} d^{-1}). Stinson and Laurie (1954) reported that flower initiation and development of African violets were inhibited when plants were grown in greenhouses and given an illuminance of no greater

than 300 footcandles during the brightest part of the day (< 2 mol m^{-2} d^{-1}). Research on the African violet which relates flowering to leaf area has not been conducted.

The objective of our research was to develop a model which would predict flowering of the African violet. Our approach was to divide the model into three components. First, a method was developed to predict which leaves formed an inflorescence in the leaf axil. Second, a model was developed which related the appearance of a visible flower bud in the leaf axil with the length of the subtending leaf blade. Third, quantitative relationships were developed which described inflorescence development rate from VB to anthesis as a function of temperature.

Materials and methods

Predicting the occurrence of inflorescence development in a leaf axil. Modeling inflorescence development of the African violet requires the ability to accurately predict which leaves will have an inflorescence develop in the leaf axil. An experiment was conducted to develop a method to predict which leaves would produce an inflorescence in the leaf axil.

One hundred twenty African violet 'Utah' plants possessing 8 to 10 leaves were transplanted into 10 cm diameter pots and were placed into four 10 m^2 glass greenhouses which were set to maintain air temperatures of 15, 20, 25, and 30C from Dec. 1990 through Feb. 1991. Each greenhouse was divided into three PPF treatments. Plants in the low PPF treatment had neutral density shade cloth placed above the plants to reduce the natural PPF by 50%. Plants in the medium PPF treatment received the natural PPF environment. The high PPF treatment had natural PPF levels plus 100 μmol m^{-2} s^{-1} from

0600 to 1800 h each day (4.3 mol m^{-2} d^{-1}) provided from 400W high pressure sodium lamps. One layer of 50% PPF reduction neutral density shade cloth was pulled over plants in all PPF treatments when the natural PPF increased above approximately 300 μmol m^{-2} s^{-1}. The average daily integrated PPF were 2.6, 4.5, and 9.5 mol m^{-2} d^{-1} for the three PPF treatments over the course of the experiment. PPF was monitored at canopy level with quantum sensors (LI-COR, LI-1909A).

The leaf axil of each leaf on a plant was examined for the presence of an inflorescence greater than 2 mm long, and the LBL of each leaf was measured after 10 flowers had opened on the plant. The percentage of leaf axils possessing an inflorescence greater than 2 mm long was calculated for each leaf number.

Leaves were numbered so that the most recently unfolded leaf at the time of transplanting was designated as leaf number zero, and each successive leaf to unfold was designated leaf number 1, 2, 3, etc... Leaves which unfolded prior to the start of the experiment were numbered, -1, -2, -3 etc..., from the second most recently unfolded to the oldest leaf.

Model development - Time to VB. The date of flower initiation in the African violet is uncertain, therefore, some physical measure other than time is necessary to predict when an inflorescence will be macroscopically visible (2 mm long) in the leaf axil. We choose to relate the time to VB to the LBL of a subtending leaf on a pre-VB plant; therefore, leaf blade measurements could be used to predict VB. Assuming that an inflorescence developed in the leaf axil of a given leaf, the time to VB would be:

$$\text{Days to VB} = (LBL_{VB} - LBL) / LER_T \qquad (1)$$

where LBL_{VB} represents the leaf blade length at VB, and LER_T represents the rate of leaf blade extension in mm d^{-1} at the particular temperature (T).

The following nonlinear function (Reed et al., 1976; Landsberg, 1977) was used to describe LER as a function of temperature:

$$LER = a(T-T_{Min})(T_{Max}-T)^b \quad (2)$$

$$a = LER_{Max}/(T_{Opt}-T_{Min})(T_{Max}-T_{Opt})^b \quad (3)$$

$$b = (T_{Max}-T_{Opt})/(T_{Opt}-T_{Min}) \quad (4)$$

where T_{Min} and T_{Max} refer to the minimum and the maximum temperature at which LER is zero. T_{Opt} is the temperature at which the optimum LER occurs, T represents the plant temperature, and LER_{Max} refers to the maximum value for LER at T_{Opt}.

A polynomial function was used to describe the LBL_{VB} as a function of temperature and daily integrated PPF:

$$LBL_{VB} = B_0 + B_1*T + B_2*T^2 + B_3*PPF_{DI} \quad (5)$$

where T represents temperature and PPF_{DI} represents the daily integrated PPF.

Model development - Time from VB to anthesis. Once VB has appeared in the leaf axil, the time until anthesis is determined by the rate of inflorescence development. Inflorescence development was quantified with a phasic development scale which identified nine stages of development. As the inflorescence of an African violet grows through the leaf canopy, the pedicel and peduncle curve to protect the primary flower

bud. The degree of curvature of the peduncle and pedicel was used to identify the stages of the phasic development scale (Figure 1 & Table 1).

The number of days required for each stage of inflorescence development was linearly related to temperature and was predicted with the following equation:

$$\text{Number of days at stage}_X = S_X * T + I_X \qquad (6)$$

where S_X equals the slope of the regression, and I_X is the intercept. T represents temperature, and X is the stage number.

The number of days required for an inflorescence to develop from any stage of development to anthesis can be predicted by integrating the number of days required for each individual stage.

$$\text{Days from stage}_X \text{ to first open flower} = \sum_{i=X}^{8} (S_i * T + I_i) \qquad (7)$$

Comprehensive flowering model. Functions (1) and (6) were combined to create a comprehensive model which predicted the number of days until the first open flower based on measurement of the LBL, daily integrated PPF, and temperature.

$$\text{Days to first open flower} = \begin{cases} \text{Eq. 1} + \text{Eq. 6} & \ldots\text{VB not present} \\ \text{Eq. 6} & \ldots\text{VB present} \end{cases} \qquad (8)$$

Parameter estimates. Linear regression was used to describe the increase in LBL from the time of leaf unfolding until the time the leaf blade extended to 40 mm. The slope of the linear regression function was calculated for leaf numbers -1 to 2.

Parameters for the nonlinear function describing LER were estimated (Table 2) using SAS procedure NLIN (SAS Institute, Inc., 1989).

Parameters for the multiple linear regression used to quantify the effect of temperature and PPF on LBL_{VB} (Table 2) and parameters for the linear regression used to quantify the time required for each stage of inflorescence development were estimated (Table 3) using SAS procedure GLM (SAS Institute, Inc., 1989).

Experimental designs : The influence of PPF on inflorescence initiation and development. One hundred African violet 'Utah' plant with 8 to 10 unfolded leaves were transplanted into 10 cm diameter pots (450 cm^3). Plants were placed into four PPF treatments in each of two walk-in growth chambers (HotPack, Model UWP 3009-2, Philadelphia, PA) which maintained plant temperatures at 26$\pm$1C DT and 23$\pm$1C NT. Plant temperature was measured by inserting a hypodermic needle thermocouple probe (Omega Hypl-30-1/2-T-G-60-SAP-M) into stem, petiole, and leaf tissue. Plant temperature was calculated as the mean temperature of the plant tissues. Cool white fluorescence lamps delivered a PPF of 23, 46, 92, or 181, μmol m^{-2} s^{-1} for 12 h d^{-1} resulting in daily integrated PPF of 1, 2, 4, or 8 mol m^{-2} d^{-1}. Layers of neutral density shade cloth were placed above the plants to produce the PPF treatments within each temperature treatment.

The leaf axil of each leaf on a plant was examined for the presence of an inflorescence greater than 1 cm long after 10 flowers had opened on the plant. The

percentage of leaf axils possessing an inflorescence greater than 1 cm long was calculated for each leaf number. Analysis of variance was performed to determine the influence of PPF on each leaf number.

Influence of the relationship between DT and NT on time to flower. Eighty African violet 'Utah' plants were placed into four walk-in growth chambers (Hotpack, Model UWP 3009-2, Philadelphia, PA) with air temperature setpoints at 15, 20, 25, and 30C. Five plants per treatment were moved between chambers at 0800 and 2000 h each day in order to create a total of 16 DT/NT treatment combinations. Cool white fluorescent lamps (Philips VHO F96T12/CW/VHO) delivered a PPF of 167 μmol m^{-2} s^{-1} for 12 h d^{-1} resulting in a daily integrated PPF of 7 mol m^{-2} d^{-1}.

The dates of anthesis were recorded for the first five flowers of each plant. A flower was considered open when the five petals formed a planar surface. Plant temperature was frequently 1 to 2C higher than air temperature during the photoperiod and 1 to 2C lower than air temperature during the dark period. Actual plant temperatures were used in regression analysis.

Influence of temperature and PPF on the time from transplant to VB. Twenty-seven African violet 'Sparkle' plants possessing 8 to 10 leaves were transplanted into 10 cm diameter pots and were placed in three growth chambers (Conviron, Model E-15) which were set to maintain plant temperature at 18, 22, and 26C. Each growth chamber was divided into three PPF treatments. Cool white fluorescence lamps (F72T12/CW/VHO) delivered a PPF of 50, 100, or 200 μmol m^{-2} s^{-1} for 12 h d^{-1} resulting in daily integrated PPF of 2.2, 4.3, and 8.7 mol m^{-2} d^{-1}. The actual

temperature of the plants in the 2.2 mol m^{-1} d^{-1} treatment within the 18C growth chamber was approximately 16C.

LBL was measured and the leaf axil was examined for the appearance of VB on all leaves every 2 to 3 days over a period of 64 days. Data were statistically analyzed as a split plot design with temperature as the main plot and PPF as the split plot. The SAS GLM procedure was used to for analysis of variance (SAS Institute, 1989).

Influence of temperature and PPF on the rate of inflorescence development from VB to anthesis. Thirty-six African violet 'Sparkle' plants with four or more developing inflorescences were placed into three growth chambers (Conviron, Model E-15, Asheville, NC) set to maintain plant temperature at 18, 22, and 26$\pm$1C. Each growth chamber was divided into three PPF treatments. Cool white fluorescence lamps (F72T12/CW/VHO) and 60W incandescent bulbs delivered a PPF of 50, 100, or 200 μmol m^{-2} s^{-1} for 12 h d^{-1} resulting in daily integrated PPF of 2.2, 4.3, and 8.7 mol m^{-2} d^{-1}.

The stage of inflorescence development, inflorescence length, and the diameter of the primary flower bud were measured every 2 to 3 days for 30 days. The time required for an inflorescence to develop through a stage was measured on the 4 to 5 inflorescences present at the start of the experiment and also on the first 2 to 3 inflorescences which appeared during the experiment. Inflorescence length was measured from the point of stem attachment to the uppermost part of the inflorescence. Data were statistically analyzed as a split plot design with temperature as the main plot and PPF as the split plot. The SAS GLM procedure was used to for analysis of variance (SAS Institute, 1989).

Greenhouse validation of the comprehensive flowering model. Twenty-four African violet 'Sparkle' plugs were placed in two greenhouses which were set to maintain air temperatures of 20 and 25C from March to May 1991. Each greenhouse was divided to provide two PPF treatments. The plants in the high PPF treatment received natural PPF, while the low PPF treatment had two layers of the neutral density cloth placed above the plants which reduced natural PPF by 75%. One layer of neutral density shade cloth (50% reduction) was pulled over the plants in both treatments when the natural PPF exceeded approximately 300 μmol m^{-2} s^{-1}. The average daily integrated PPF for the high and low PPF treatments over the time of the experiment was 3.2 and 8.2 mol m^{-2} d^{-1}, respectively. The average plant temperature in the two greenhouses over the time of the experiment was 21.5 and 25.0C.

LBL, stage of inflorescence development, and inflorescence length were measured three times per week.

Data collected during the validation were used to test the model's prediction of the time of VB and anthesis for individual inflorescences. LBL at the time of transplant was used to predict the number of days to VB of leaf numbers -3, -2, -1, and 0. LBL at the time of leaf unfolding was used to predict the number of days to VB of the first five leaves which unfolded during the experiment, i.e. leaf numbers 1 through 5. The date of VB was used to predict the number of days to anthesis for each inflorescence developing in the axils of leaf numbers -3 to 5.

General procedures. The plants grown in all of the experiments were subirrigated with a nutrient solution consisting of 3.6 mmol N and 1.3 mmol K from calcium and potassium nitrate. Electrical conductivity of the media in the root zone was maintained

between 0.5 and 1.0 mS using the 2:1 water/soil (vol/vol) method (Warncke and Krauskopf, 1983). Phosphoric acid was included in the nutrient solution as needed to maintain media pH between 5.5 and 6.5.

Results

The occurrence of an inflorescence developing in the leaf axil. The occurrence of an inflorescence developing in the axil of a leaf was related to the age of the leaf at transplanting (Figure 2). Inflorescences did not developed in the axils of leaf numbers -12 to -7. The percentage of leaves forming an inflorescence increased from 0 to 100% as leaf number increased from -6 to -1, was 100% for leaves -1 to 2, and then decreased back to 0% as leaf number increased from 2 to 9.

The percentage of leaves with inflorescences was also correlated with leaf size at the time of data collection (Figure 2). Leaf blades which grew to 40 mm in length or more formed inflorescences in more than 60% of the leaf axils. The six oldest leaves at transplant failed to grow to more than 30 mm in length after transplant, and inflorescences did not develop in their leaf axils. LBL increased from 30 to 52 mm as leaf number increased from -6 to 0, and the occurrence of inflorescences increased from 0 to 100%. LBL decreased from 52 to 12 mm as leaf number increased from 1 to 13 and the occurrence of inflorescences decreased from 100% to 0%.

The influence of PPF on inflorescence initiation and development. The percentage of inflorescences developing in the leaf axils increased as the daily integrated PPF increased from 1 to 4 mol m^{-2} d^{-1} (Figure 3). Increasing the daily integrated PPF from 4 to 8 mol m^{-2} d^{-1} did not result in any further increase in flower initiation and

development. Leaf number -1 was the first leaf to consistently produce an inflorescence in 100% of the leaf axils.

The effect of the DT and NT relationship on time to flower. The number of days from transplant to flower was a function of ADT (Figure 4), not the relationship between DT and NT; therefore, ADT was used to develop the flowering model. Leaves of plants grown at 30C DT were chlorotic, and inflorescences did not develop.

Time of VB appearance in the leaf axil. LBL was a linear function of time from 7 mm to approximately 40 mm in length for all experimental treatments (Figure 5). The slope of the linear regression line represented the LER for a given leaf. The maximum rate of leaf extension was estimated at 1.26 mm day^{-1} which occurred at 24.0C (Figure 6). T_{Min} and T_{Max} for LER were estimated at 13.8 and 29.0C, respectively.

LBL_{VB} was influenced by temperature and daily integrated PPF (Figure 7). A polynomial function was used to describe the influence of temperature and daily integrated PPF on LBL_{VB}. LBL_{VB} increased as temperature increased from 18 to 22, then decreased as temperature was increased further to 26C. Final LBL displayed similar response to temperature (data not shown). LBL_{VB} decreased as the daily integrated PPF increased from 2.2 to 8.7 mol m^{-2} d^{-1}.

A model based on measured LBL and LER was created to predict the time required before the appearance of VB in the leaf axil (Eq. 1). The predicted number of days before VB appeared in the axil a leaf which had a 6 mm long leaf blade decreased from 47 to 29 days as temperature increased from 18 to 26C (Figure 8).

Time from VB to anthesis. A phasic development scale was developed to describe inflorescence development from VB to anthesis (Table 1 & Figure 1). Linear functions

were utilized to describe the number of days required for an inflorescence to pass through each developmental stage (Figure 9). A model based on current stage of development and temperature was created to predict time to anthesis from any stage of development (Eq. 7). The predicted number of days from VB to anthesis decreased from 40 to 28 as temperature increased from 18 to 26C (Table 4).

Inflorescence length and bud diameter increased with respect to the developmental stage (Figure 10 A & B). Temperature and PPF did not influence inflorescence height or bud diameter at each stage of development.

Greenhouse model validation. The comprehensive flowering model accurately predicted the time to VB and time from VB to anthesis (Figure 11A, B, & C). A distribution of the deviation between the observed and the predicted number of days show that the model had the tendency to overpredict the actual time required (Figure 12A, B, C).

Discussion

Leaf area and PPF influence the ability of a leaf to become a strong source of photosynthates. Transplanting a plant from an environment where there is strong competition with surrounding plants for photons and the container capacity of the media is relatively low to an environment where the competition between neighboring plants for photons has been removed and the container capacity has increased tenfold influences leaf expansion and the capacity of the leaf to intercept photons. Consequently, leaves which unfold and expand prior to transplant do not expand to their full size, while the youngest leaves at the time of transplant and the leaves which expand after transplant will expand

to their full size. As a result, the youngest leaves at the time of transplant will be the first leaves to have the capacity to become a strong source of photosynthates, thus a high percentage of these leaves will have an inflorescence develop in the leaf axil.

Most commercial producers of African violets purchase small plants from a propagator. The small plants are then transplanted and grown until they flower, usually 3 to 4 months after transplant. The developmental status of a small plant when received by the grower can vary due to the age of the plants and the methods of production by the propagator. The model presented in this paper will be useful for predicting anthesis of a crop at the time of transplant and for tracking the progress towards anthesis. The use of the inflorescence development model requires estimation of the first leaf to form an inflorescence. The proposed method of determining the first leaf to form an inflorescence, i.e. using leaf number -1, is based on the assumption that flower initiation has not occurred prior to transplanting. Destructive examination of the leaf axils prior to transplant occasionally reveals that flower initiation has already occurred on some of the plants. Consequently, a model must be developed which will predict the first leaf to produce an inflorescence based on the developmental status of the plants at the time of transplant.

Once an inflorescence is visible in the leaf axil, the rate at which the inflorescence develops to anthesis was a function of temperature. A phasic development scale was used in our model to predict anthesis. However, inflorescence height and bud diameter could have also been used. Our observations indicate that inflorescence height and bud diameter are influenced by cultivar, thus a model based on inflorescence length and bud diameter would not accurately predict anthesis for many cultivars.

Plants grown in growth chambers with fluorescent and incandescent lamps have leaves which are less pliable than leaves of plants grown under natural PPF with the same PPF. As a result, the inflorescence is met with greater resistance as it penetrates the leaf canopy. We observed that the number of days required for an inflorescence to pass through Stage 5 during the model development experiment performed in a growth chamber appeared to be higher than in the greenhouse validation experiment. This potential error may explain the tendency of the flowering model to overpredict the number of days form VB to anthesis.

In summary, the time required for an African violet to flower was divided into two steps: 1) the time from transplant to the appearance of a VB in the leaf axil of the plants 2) the time from VB to anthesis. Assuming that flower initiation has not occurred prior to transplanting, an inflorescence will develop in the second most recently unfolded leaf at the time of transplanting when the plant is provided a daily integrated PPF of $\geq$2 mol m^{-2} d^{-1}. An inflorescence will be macroscopically visible in the leaf axil when the leaf blade of this leaf extends to approximately 39 to 45 mm long, depending on the temperature and PPF environment; therefore, the time required to the appearance of VB in the leaf axil is dependent on the rate at which the leaf extends, which a function of temperature. A phasic development scale was created to describe the current developmental status of an inflorescence. The number of days required for an inflorescence to develop through each stage of inflorescence development was described as a linear function of temperature from 18 to 26C.

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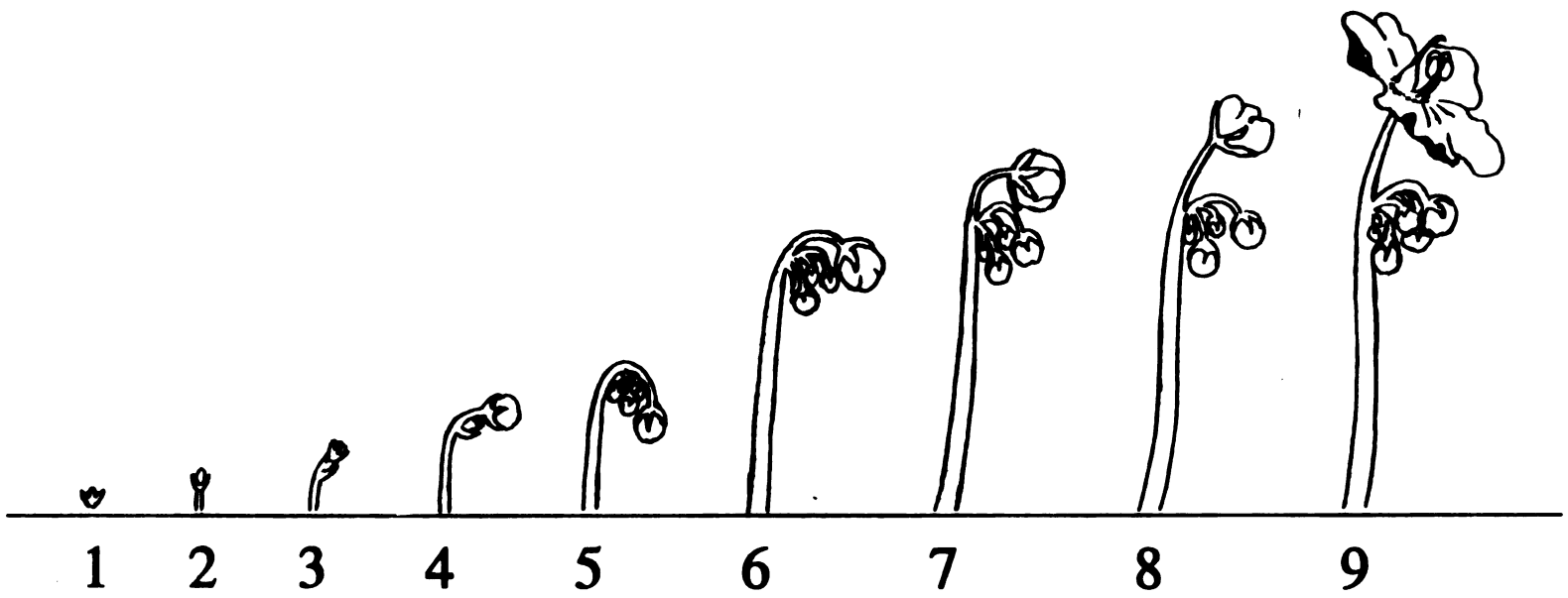
Figure 1. Phenology of the inflorescence development. Each drawing corresponds to a stage of development described in Table 1.



Stage of Inflorescence Development

Figure 2. Correlation between LBL and the percentage of leaf axils forming an inflorescence with respect to leaf number.

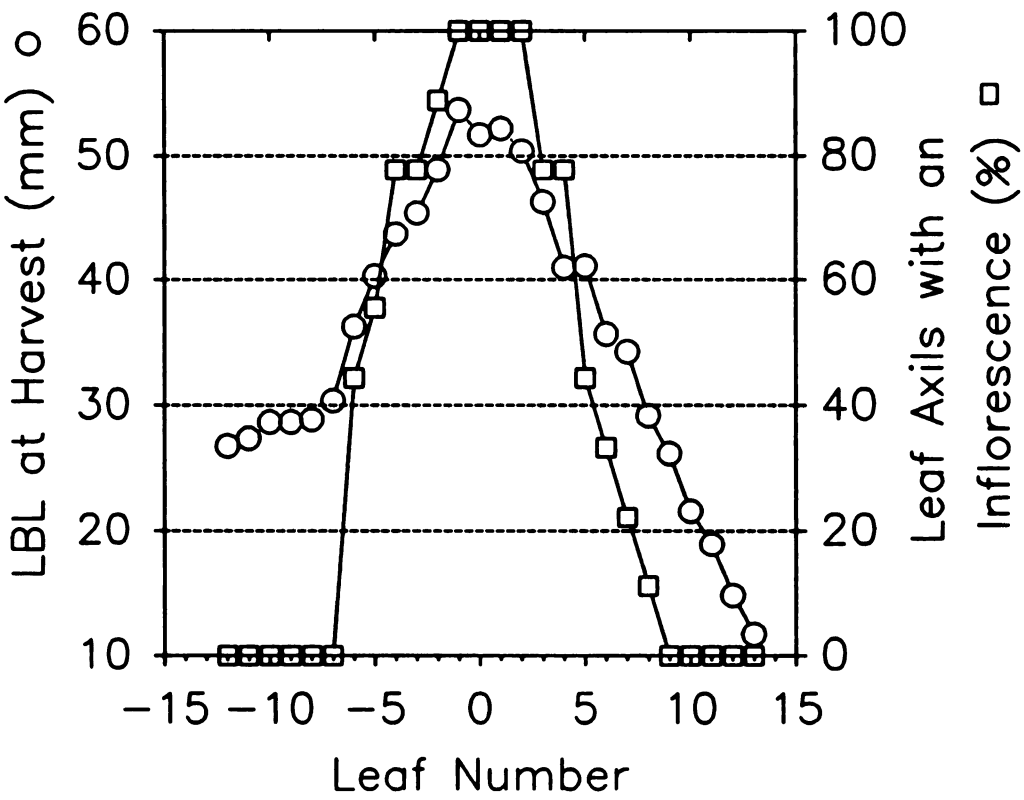

LBL at Harvest (mm) o
60
50
40
30
20
10
100
80
60
40
20
0
Leaf Axils with an Inflorescence (%) □
−15 −10 −5 0 5 10 15
Leaf Number

Figure 3. The influence of daily integrated PPF on the percentage of leaf axils forming an inflorescence with respect to leaf number.

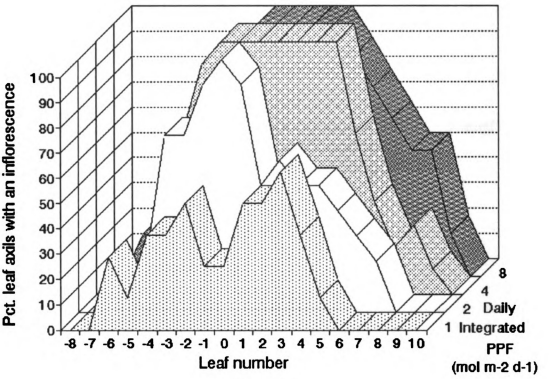

Pct. leaf axils with an inflorescence
100
90
80
70
60
50
40
30
20
10
0
-8 -7 -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 7 8 9 10
Leaf number
8
4
2
1
Daily Integrated PPF (mol m-2 d-1)

Figure 4. The number of days to flower shown as a function of average daily temperature. Data points and error bars represent treatment means and 95% confidence intervals.

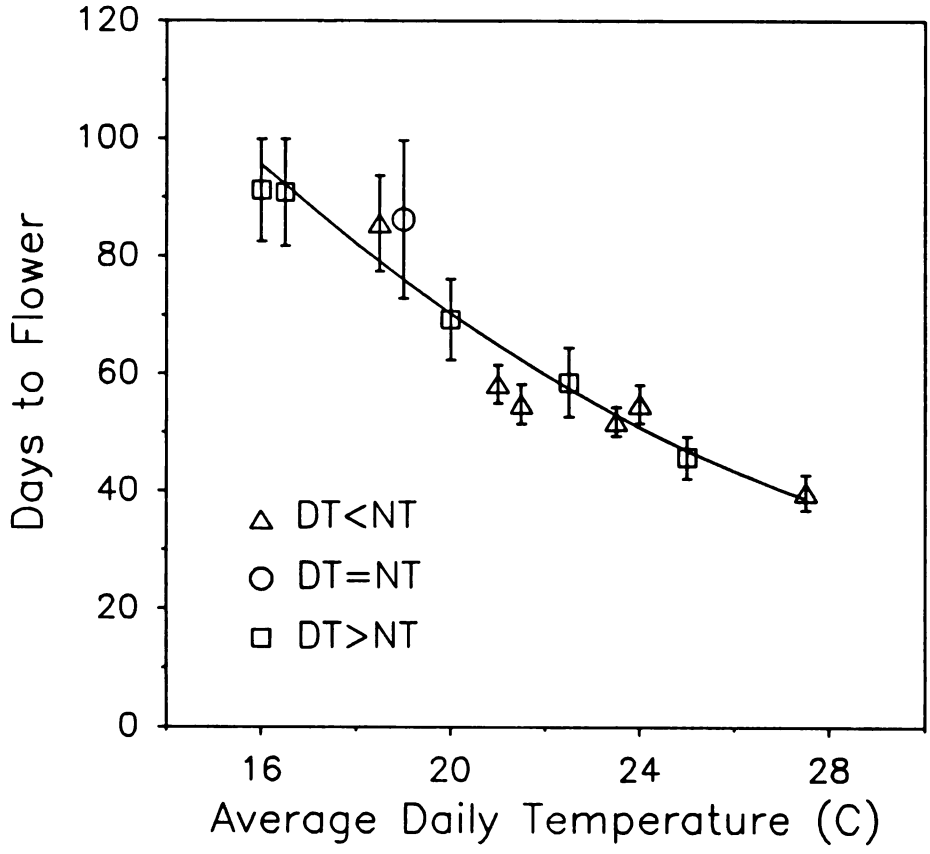

120
100
80
60
40
20
0
Days to Flower
DT<NT
DT=NT
DT>NT
16
20
24
28
Average Daily Temperature (C)

Figure 5. The slope of the regression line ($Y=0.913*X+3.68$) represents the rate of leaf extension over time during the first 40 mm of leaf extension for an individual leaf ($R^2=0.99$).

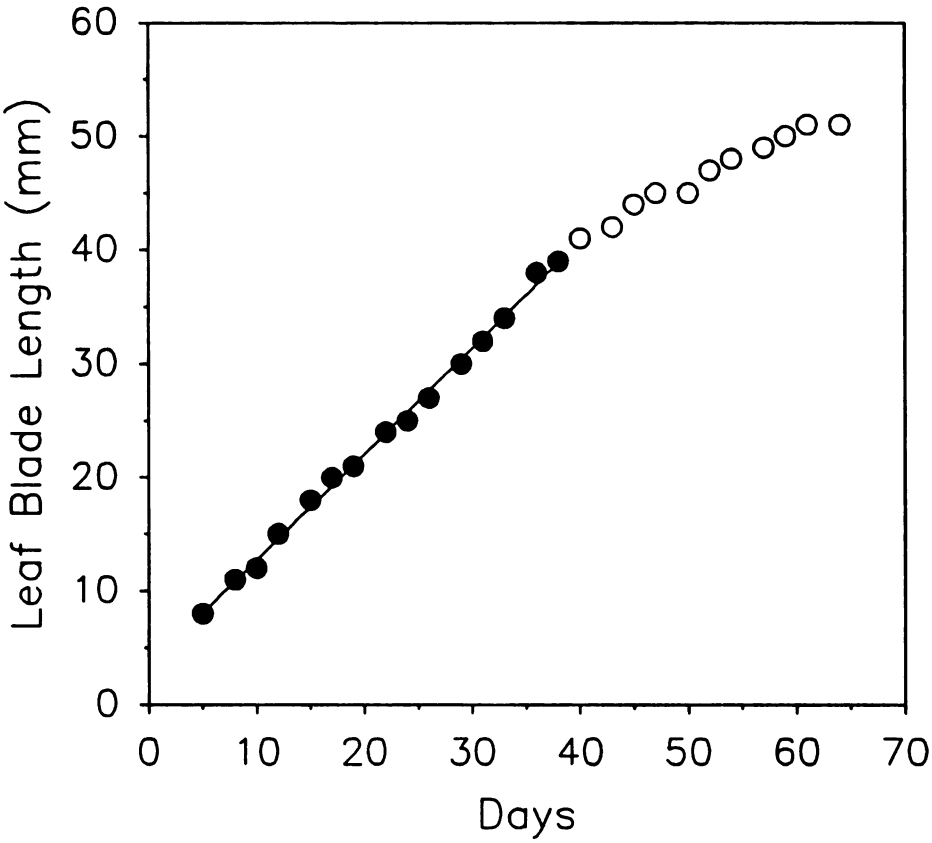

Leaf Blade Length (mm)
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
Days

Figure 6. The rate of leaf extension shown as a function of temperature. Data points represent the treatment means after the data from the PPF treatments were pooled at each temperature, and error bars display the 95% confidence intervals.

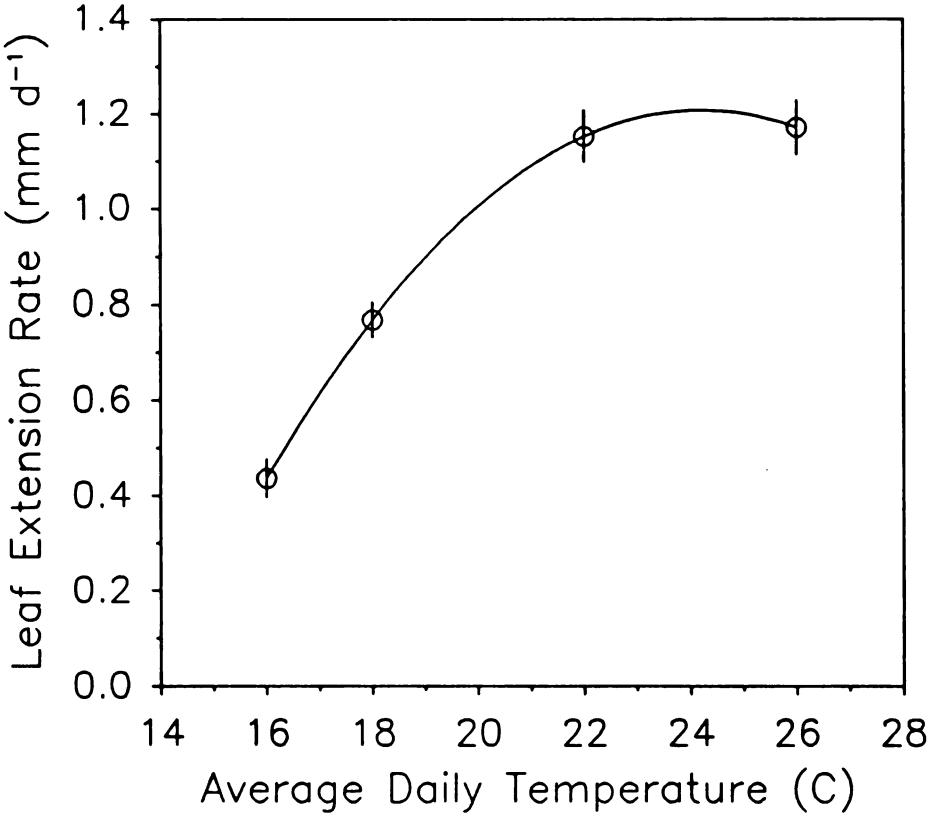

Leaf Extension Rate (mm d-1)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
14
16
18
20
22
24
26
28
Average Daily Temperature (C)

Figure 7. A model describing the influence of daily integrated PPF and temperature on LBL_{VB}.

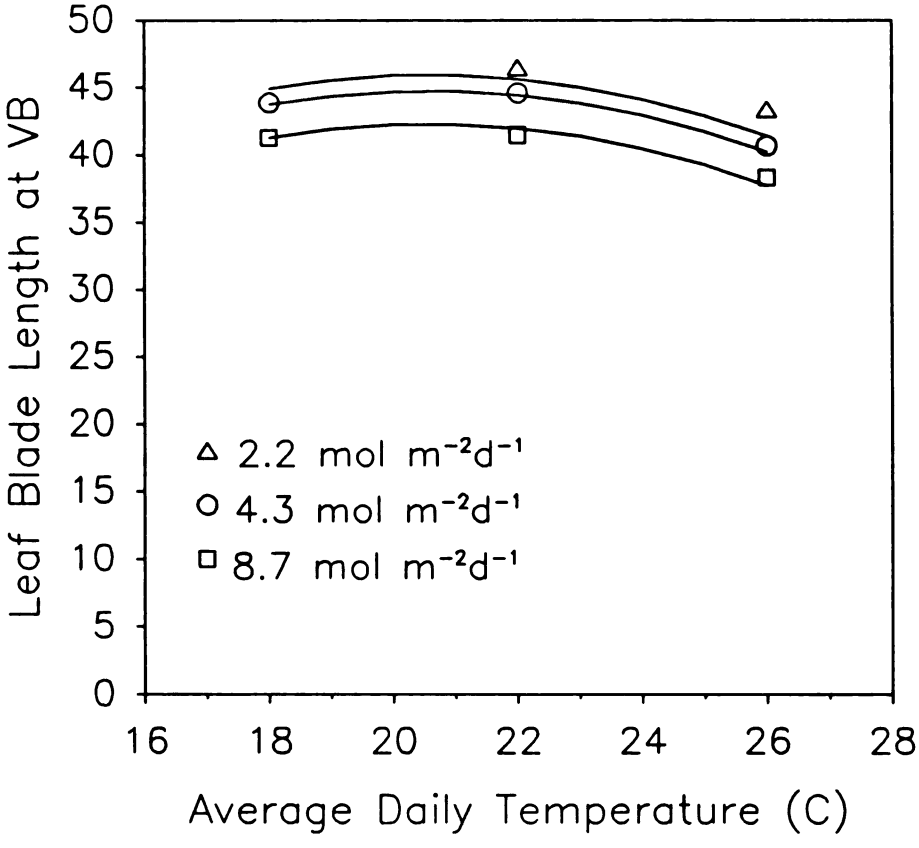

Leaf Blade Length at VB
50
45
40
35
30
25
20
15
10
5
0
16
18
20
22
24
26
28
Average Daily Temperature (C)
2.2 mol m-2d-1
4.3 mol m-2d-1
8.7 mol m-2d-1

Figure 8. Surface response of the predicted number of days to VB as influenced by temperature and measured LBL.

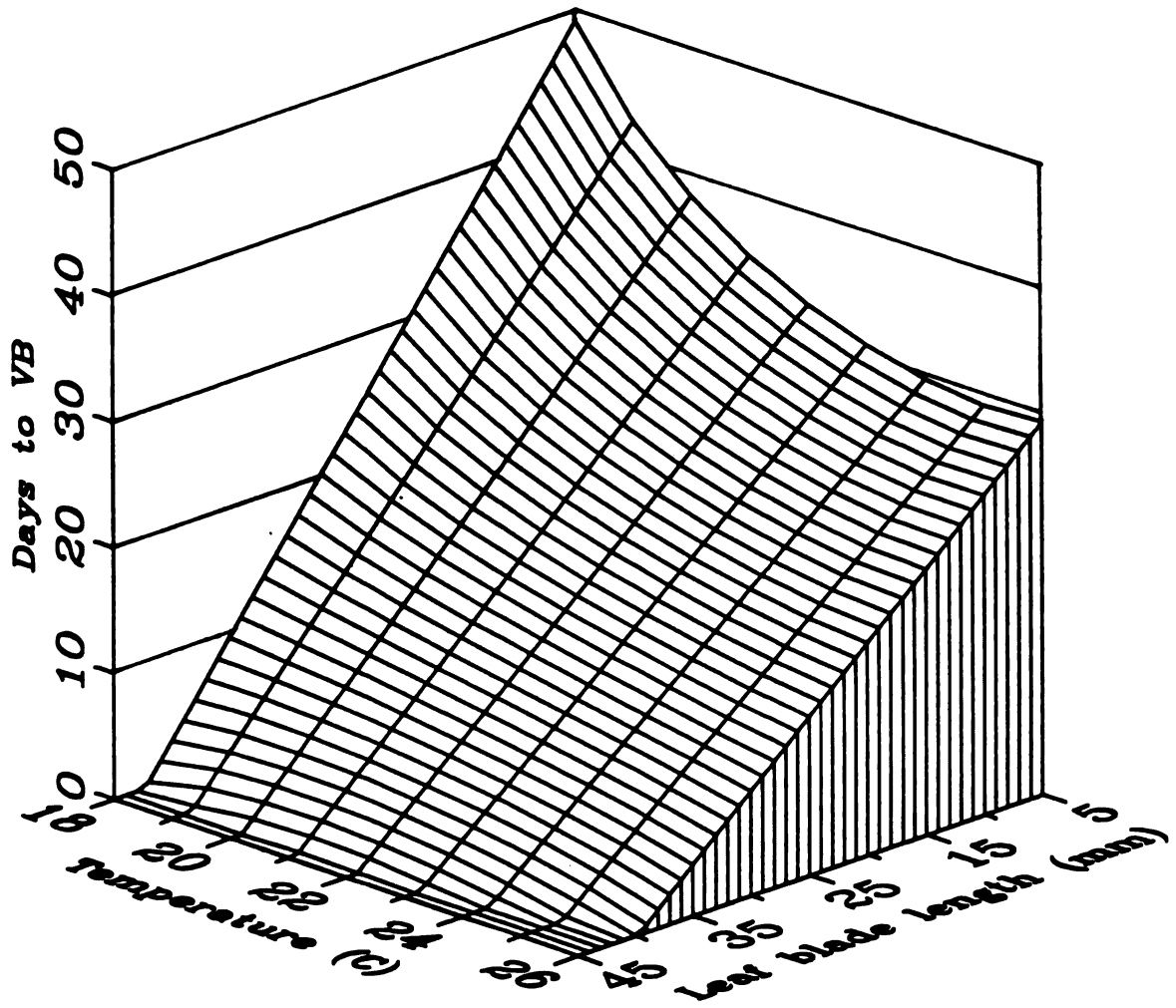

Days to VB
0
10
20
30
40
50
18
20
22
24
26
Temperature (C)
45
35
25
15
5
Leaf blade length (mm)

Figure 9. The influence of temperature on the number of days for an inflorescence to develop through each stage of development. Symbols represent treatment means and error bars represent the 95% confidence intervals.

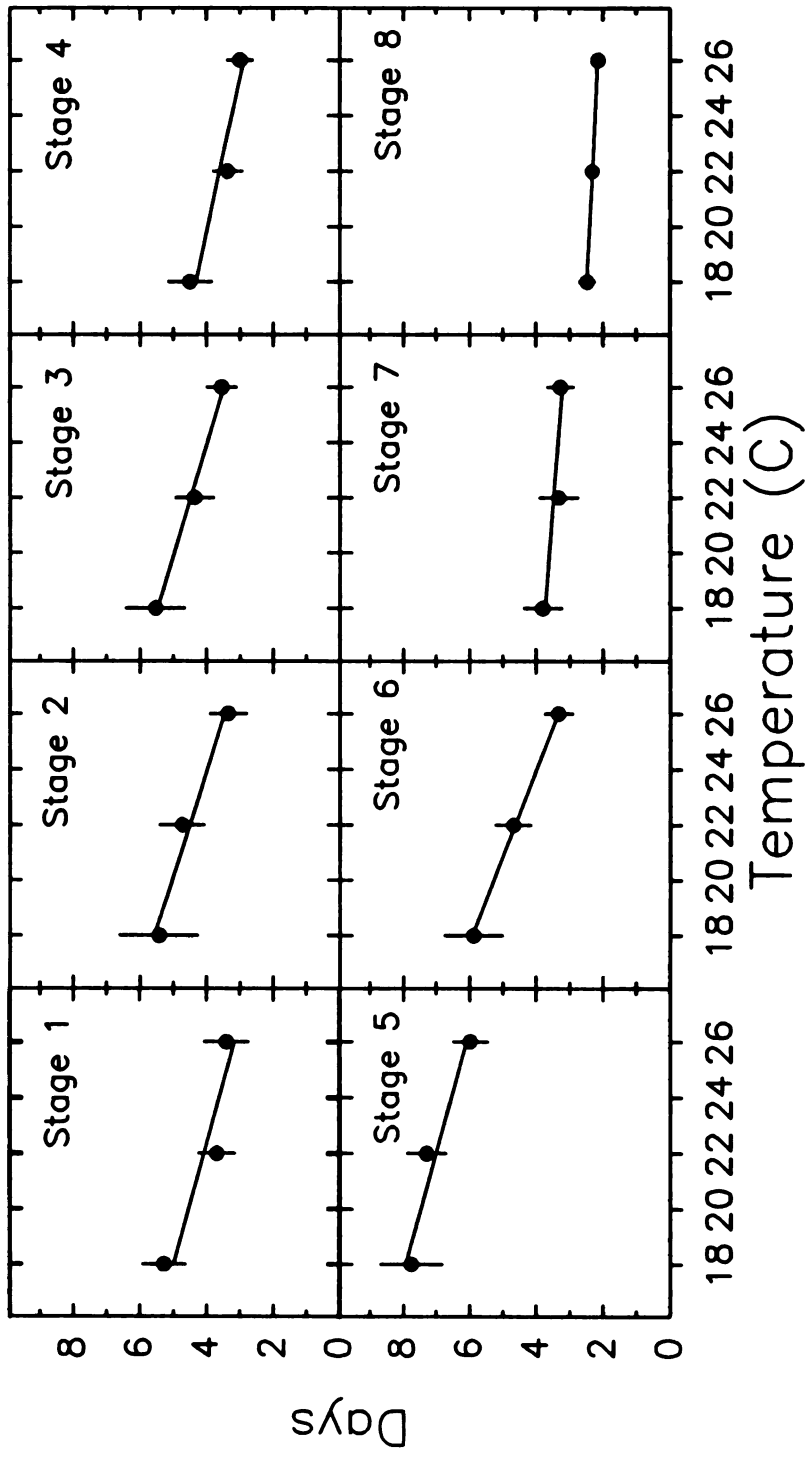

Stage 1
Stage 2
Stage 3
Stage 4
Stage 5
Stage 6
Stage 7
Stage 8
Days
0
2
4
6
8
18 20 22 24 26
Temperature (C)

Figure 10. The observed A) primary bud diameter and B) inflorescence length at each stage of inflorescence development. Data from all temperature and PPF treatments were pooled. Data points and error bars represent the mean values and 95% confidence intervals for all treatments.

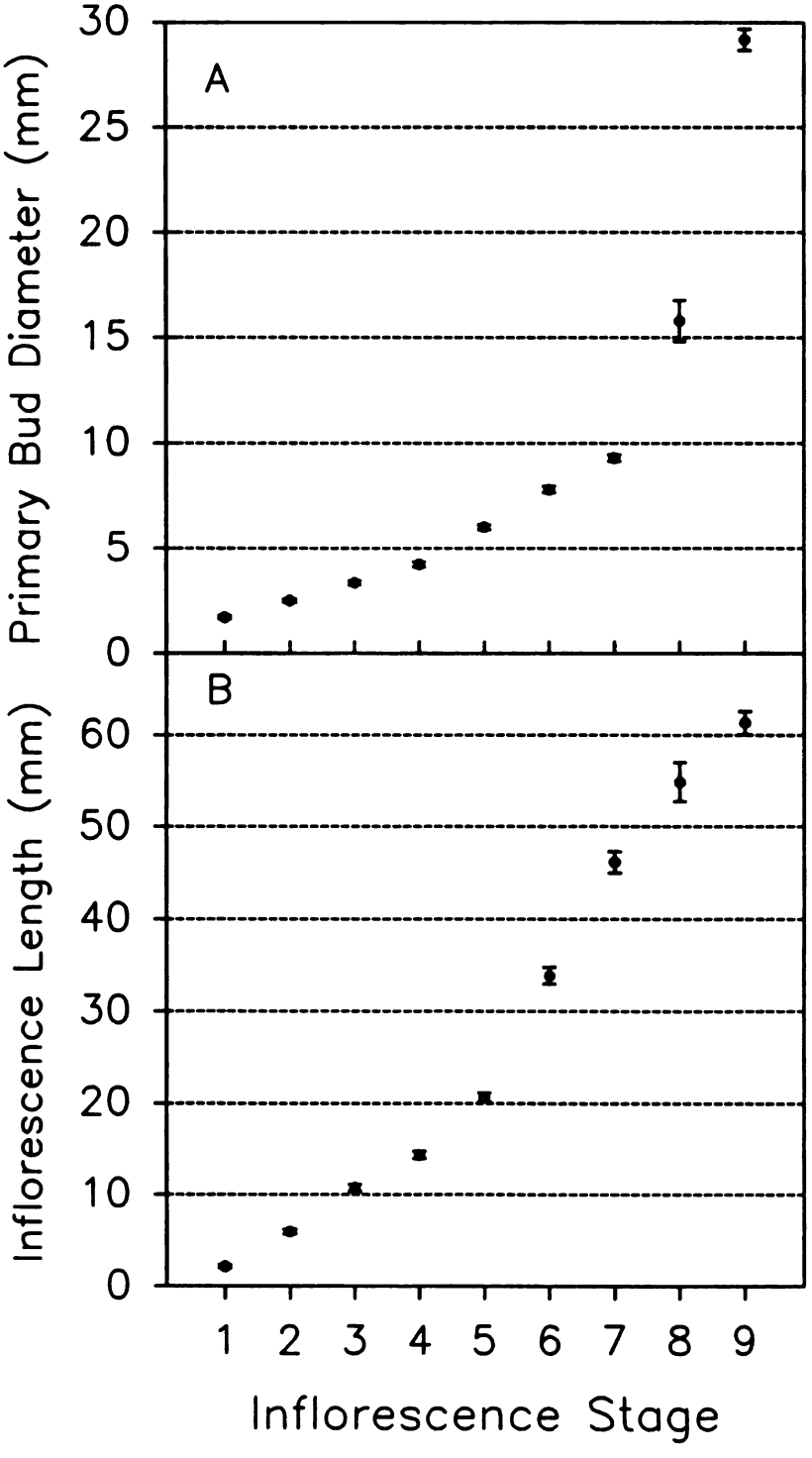

A
B
Primary Bud Diameter (mm)
Inflorescence Length (mm)
Inflorescence Stage
0
5
10
15
20
25
30
0
10
20
30
40
50
60
1
2
3
4
5
6
7
8
9

Figure 11. Comparison between the observed (o) and the predicted (solid line) number of days from A) the initial LBL measurement to the time of appearance of VB in the leaf axil, B) the number of days from VB to anthesis, and C) the number of days from the initial LBL measurement to anthesis.

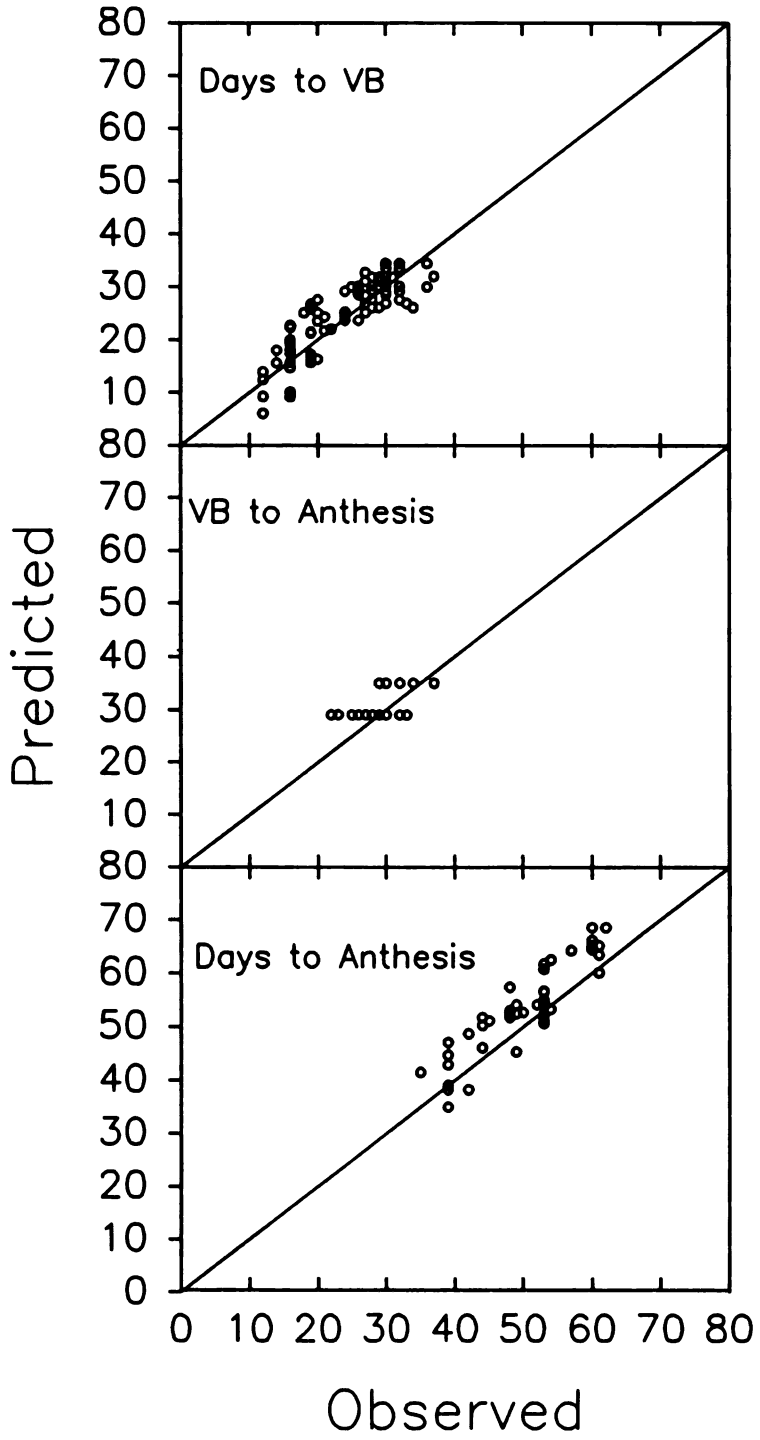

Days to VB
VB to Anthesis
Days to Anthesis
Predicted
Observed
0 10 20 30 40 50 60 70 80

Figure 12. Distribution of the deviation between the observed and the predicted number of days from A) the initial LBL measurement to the time of appearance of VB in the leaf axil, B) the number of days from VB to anthesis, and C) the number of days from the initial LBL measurement to anthesis.

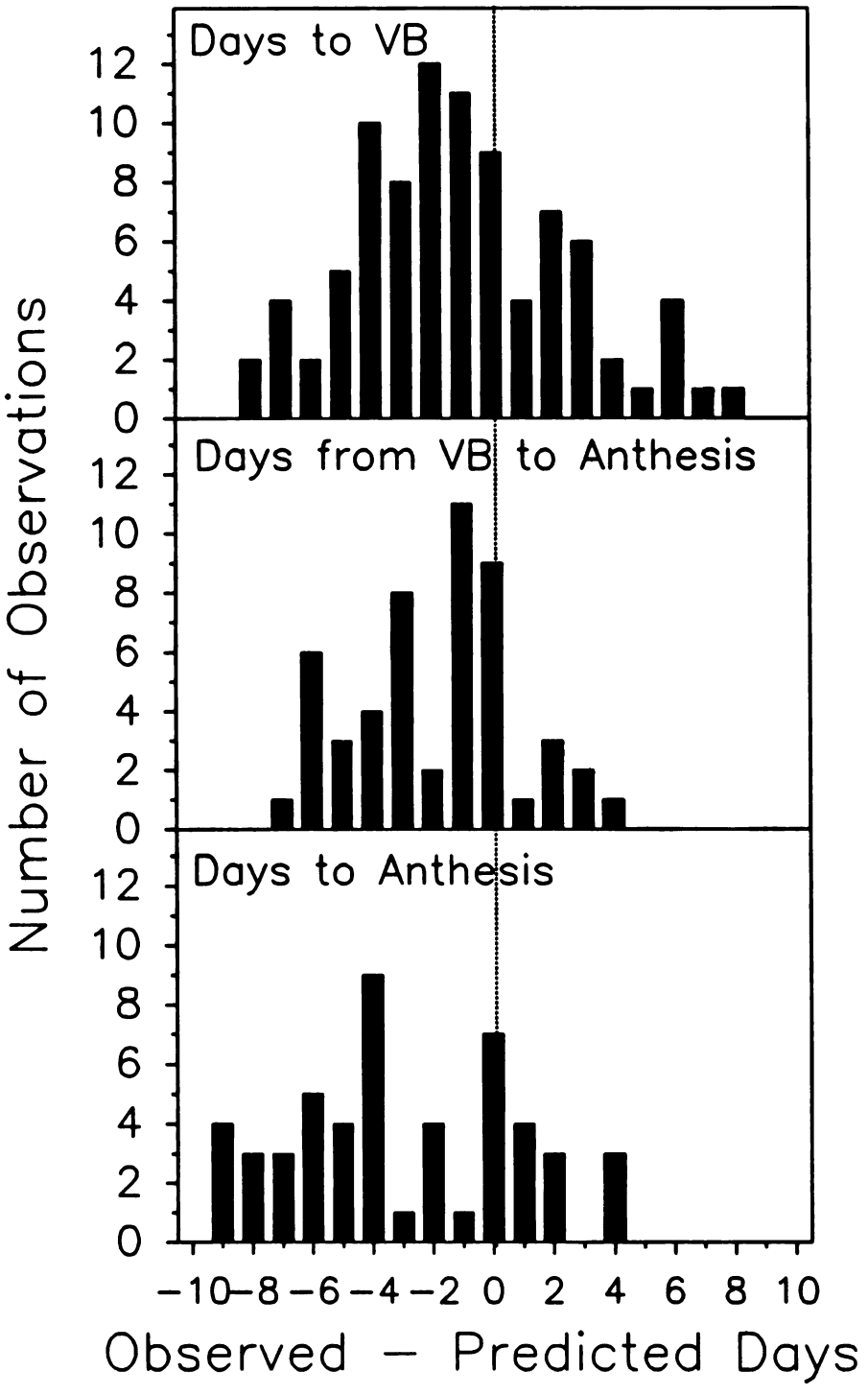

Days to VB
Days from VB to Anthesis
Days to Anthesis
Number of Observations
0
2
4
6
8
10
12
−10 −8 −6 −4 −2 0 2 4 6 8 10
Observed − Predicted Days

Table 1. Phenological description for each stage of inflorescence development.

Stage	Phenological description of inflorescence development
1	Reproductive bud becomes visible (2 mm) in the leaf axil
2	The peduncle subtending the primary bud becomes visible
3	The peduncle begins to curve
4	The pedicel has curved at a 90° angle with respect to the peduncle
5	The pedicel has curved at an angle less than 90° with respect to the peduncle, and the secondary buds are located at the highest point of the inflorescence
6	The primary bud and pedicel have begun to increase the angle with respect to the peduncle, the pedicel is located at the highest point of the inflorescence, and the primary bud begins to push through the leaf canopy
7	The upper half of the pedicel and the primary bud are at a 90° angle with respect to the lower half of the pedicel
8	The upper half of the pedicel has begun to straighten out, and the petals have begun to unfold.
9	All five petals are reflexed and are at a 180° angle with respect to each other

Table 2. Parameter estimates for nonlinear (LER) (Eqs. 2-4) and polynomial (LBL_{VB}) (Eq. 5) submodels of the time to VB model.

Model	Parameter	Estimate	Asymptotic 95% confidence interval	
			Lower	Upper
LER	T_{Min}	13.8	11.6	15.9
	T_{Max}	29.0	16.99	41.02
	T_{Opt}	23.96	22.8	25.12
	LER_{Max}	1.26	1.10	1.42
LBL_{VB}			Std. Error of Estimate	
	b_0	-18.46	20.39	
	b_1	6.38	1.83	
	b_2	-0.155	0.04	
	b_3	-0.564	0.118	

Table 3. Parameter estimates for the linear functions describing the number of days required for each stage of inflorescence development (Eq. 6).

Stage	Parameter	Estimate	95% Confidence Intervals	
			Lower	Upper
1	S_1	0.23	0.11	0.35
	I_1	9.16	6.57	11.75
2	S_2	0.26	0.11	0.41
	I_2	10.31	6.70	13.93
3	S_3	0.25	0.14	0.36
	I_3	9.93	6.80	13.06
4	S_4	0.18	0.09	0.27
	I_4	7.59	4.93	10.25
5	S_5	0.23	0.11	0.35
	I_5	12.08	8.32	15.84
6	S_6	0.32	0.22	0.42
	I_6	11.69	8.31	15.07
7	S_7	0.06	-0.03	0.15
	I_7	4.90	2.28	7.52
8	S_8	0.04	0.01	0.07
	I_8	3.23	2.43	4.03

Table 4. The predicted number of days for an inflorescence to develop to anthesis based on the current stage of inflorescence development and temperature (Eq. 7)

Temp. (C)	Stages of inflorescence development								
	1	2	3	4	5	6	7	8	9
18	40	35	30	24	20	12	6	2	0
20	37	32	28	22	18	11	6	2	0
22	34	30	26	21	17	10	6	2	0
24	31	27	23	19	16	9	5	2	0
26	28	25	21	18	15	9	5	2	0